37

P
Sci
B

MEMOIRS

READ BEFORE THE

BOSTON SOCIETY OF NATURAL HISTORY;

BEING A NEW SERIES

OF THE

BOSTON JOURNAL OF NATURAL HISTORY.

VOLUME V.

69120
6/4/06

BOSTON:
PUBLISHED BY THE SOCIETY.
1895–1904.

PUBLISHING COMMITTEE.

WILLIAM G. FARLOW,
JOHN S. KINGSLEY,
CHARLES S. MINOT,
J. B. WOODWORTH,
GLOVER M. ALLEN.

CONTENTS OF VOLUME V.

1. On the reserve cellulose of the seeds of Liliaceae and of some related orders. Plate 1–6. *By Grace E. Cooley.* (Published July, 1895.) 1
2. Notes on the dissection and brain of the chimpanzee "Gumbo" (Troglodytes niger). Plate 7–10. *By Thomas Dwight.* (Published October, 1895.) 31
3. Synapta vivipara: a contribution to the morphology of echinoderms. Plate 11–15. *By Hubert Lyman Clark.* (Published January, 1898.) 53
4. Localized stages in development in plants and animals. Plate 16–25. *By Robert Tracy Jackson.* (Published April, 1899.) 89
5. The development, structure, and affinities of the genus Equisetum. Plate 26–30. *By Edward C. Jeffrey.* (Published April, 1899.) 155
6. The anatomy and development of Cassiopea xamachana. Plate 31–38. *By Robert Payne Bigelow.* (Published August, 1900.) 191
7. Description of the human spines showing numerical variation in the Warren museum of the Harvard medical school. *By Thomas Dwight.* (Published January, 1901.) 237
8. Observations on living Brachiopoda. Plate 39–61. *By Edward S. Morse.* (Published July, 1902.) 313
9. The skeletal system of Necturus maculatus Rafinesque. Plate 62–67. *By Harris Hawthorne Wilder, Ph. D.* (Published January, 1903.) 387
10. The comparative anatomy and phylogeny of the Coniferales. Part 1.—The genus Sequoia. Plate 68–71. *By Edward C. Jeffrey.* (Published November, 1903.) . . . 441
11. Fossil footprints of the Jura-Trias of North America. Plate 72. *By Richard Swann Lull, Ph. D.* (Published April, 1904.) 461

Index. 559

MEMOIRS

READ BEFORE THE BOSTON SOCIETY OF NATURAL HISTORY.

1. ON THE RESERVE CELLULOSE OF THE SEEDS OF LILIACEAE AND OF SOME RELATED ORDERS.

By GRACE E. COOLEY.

Read March 20, 1895.

INTRODUCTION.

IN this study of the seeds of Liliaceae, I employ the term *reserve cellulose* in the natural logical sense, for the material laid down on the walls of the endosperm of many seeds, which is known to disappear as food for the seedling during germination. The term has been used by Reiss[1] in a chemical sense, for the substance of the plant cell wall which, by hydrolysis, yields seminose (mannose). He has distinguished two reserve substances, which are to be found on the walls of the cells in the endosperm of seeds. One of these, reserve cellulose, yields seminose, later found to be identical with mannose; the other, which he calls amyloid, does not yield mannose, by hydrolysis, and is colored blue by iodine without the action of other agents. Schulze[2] has included in a more general term, hemicellulose, those constituents of the cell membrane of plants, which are easily soluble in weak, hot, mineral acids, and which yield glucose.

He has further shown, in the same article, that some plant membranes yield mannose together with some other sugar, as in the coffee bean and seeds of the date. Winterstein[3] has found amyloid associated with hemicellulose in certain plant membranes.

---

[1] Reiss, Ueber die natur der reservecellulose. Landw. jahrbücher, 18, s. 711.

[2] E. Schulze, Zur kenntniss der chemischen zusammensetzung der pfl[illegible] chem [illegible]

[3] F. W[illegible]

My own microchemical studies would lead to the inference, that the reserve material of the seeds of Liliaceae is, in some cases at least, a complex body, and, until we understand its chemical nature better, it is more convenient for botanists to employ a term which shall not entangle them in chemical difficulties. Hence, in this work, reserve cellulose is the material stored on the walls of the endosperm cells, which is to be distinguished from the original membrane, and which is used up during germination.

The unfailing chemical characteristic of the reserve cellulose, of all the seeds examined, is its easy solubility with hot, weak, mineral acids; a characteristic which points to the conclusion that the reserve cellulose of the Liliaceae is Schulze's hemicellulose.

The methods of microchemical research are as yet too crude to follow exactly, under the microscope, the history of a substance like reserve cellulose, from the time of its appearance in the seed, until it finally disappears during germination; but it cannot be without good results to investigate and record such phenomena as are open to us, and I have, under the advice and suggestion of Professor Dodel and Dr. Overton, attempted the present work, in the hope of opening up the subject, by a general review of the main facts, to more minute study.

I shall first speak of the distribution of reserve cellulose in the Liliaceae and some allied orders, describing its general appearance. In the second part of the work, I have sought to point out the behavior of the substance in the presence of microchemical tests. Following this, is the history of reserve cellulose during the germination of the seed; and, lastly, its origin and growth in the ripening seed are described.

THE OCCURRENCE OF RESERVE CELLULOSE IN THE SEEDS OF LILIACEAE AND RELATED ORDERS.

The seeds of Liliaceae belong to that class of monocotyledonous seeds which are furnished with a large endosperm and a comparatively small embryo. The endosperm consists, in many species, of cells with thick walls, the thickening being produced, as I hope later to show, by a substance which is laid down as a secondary structure during the ripening of the seed, and which is used up during the period of germination as nourishment for the young plant. This reserve material, to which I have applied the term reserve cellulose, has been found in the endosperm of the ripe seeds of the twenty-two genera of Liliaceae which I have examined. It is also found to occur in two genera of Amaryllidaceae and in four of Iridaceae.

The seeds of Liliaceae which were examined are from [illegible] represent all of the endemic tribes but one, and thirteen of the [illegible] into which Engler and Prantl divide the order.

From its universal occurrence in these thirteen families, [illegible] not closely related, but range from the beginning of the system to the [illegible] the wide distribution of reserve cellulose in the Lily family.

Seeds of the following plants were examined and found to contain reserve cellulose.

Liliaceae; Tofieldia calyculata, Wahlnb. Galtonia candicans, Decsne.
Colchicum autumnale, L. Ornithogalum [illegible]
Asphodelus luteus, L. Muscari botryoides, DC.
Antericum liliago, L. Asparagus officinalis, L.
Allium cepa, L. Smilacina racemosa, Desf.
ursinum, L. trifolia, Desf.
Lilium martagon, L. Polygonatum multiflorum, All.
Fritillaria imperialis, L. Convallaria majalis, L.
Tulipa gesneriana, L. Streptopus amplexifolius, DC.
Lloydia serotina, L. Paris quadrifolia, L.
Scilla sibirica, Andrs. Trillium ovatum, Pursh.
Hosta caerulea, Tratt. Smilax auriculata, Walt.
Amaryllidaceae; Galanthus nivalis, L. Narcissus pseudo-narcissus, L.
Iridaceae; Iris sibirica, L. Crocus vernus, All.
pseudacorus, L. Gladiolus sp. ?
Belamcanda chinensis, Adans.

The general appearance of the cells of the endosperm of Polygonatum is typical of many of the plants mentioned.

A radial section of the seed gives a section of the endosperm cells in the plane of their long axes. The cells are long, with parallel walls, and are radially arranged about the embryo.

The walls are thickened so much as, in many cases, to occupy one half the original cell-lumen. They are white and glistening, and the primary cell membrane, on account of its different refractive power, shows as a dark line clearly outlining the original cells. The contiguous cells preserve connection with one another, as far as the membrane, by canals which penetrate the thickenings.

The cell contents are of granular reserve protein matters and oil; the nucleus is to be seen. Pl. 1, fig. 1, shows a few of these cells.

Cells of *Iris pseudacorus*, *Asparagus officinalis*, etc., present much the same appearance. In Pl. 1, fig. 2, a cell from the endosperm of *Iris pseudacorus* is shown.

Sections tangential to the seed give, of course, a transverse section, or one oblique to the long axis of the cell. The form of the cell in this view is, in general, hexagonal, and such a section brings into view the surface of the cell walls, where the canals appear as disks or pits. (Compare Pl. 2, fig. 6.) In Ornithogalum, Galtonia, and Hosta (Pl. 1, figs. 3, 4, and 5), the walls of the endosperm cells are not greatly thickened, and the canals are more frequent. They give a truer picture of the nature of the thickening, for they appear as processes grown from the wall into the lumen of the cell.

The cells in Tulipa, Allium, and others have very few canal connections between them, and the walls are much thickened, so as to give the appearance of granular cell contents, imbedded in a homogeneous mass of cellulose substance. No primary membrane appears, and the cell contents are evenly granular. Pl. 1, figs. 6 and 7, are sketches of Tulipa seeds cut in the radial, and in the transverse direction, and viewed with different magnifying powers.

In Paris, the thickenings of the endosperm cells are slight and appear mainly at the angles. Pl. 1, fig. 8, illustrates the endosperm cells of Paris.

Pl. 1, fig. 9, is a view of the cells when water has somewhat swelled the reserve cellulose. These cells differ from all the others mentioned, in that they contain starch. Lloydia (Pl. 1, fig. 10) also contains starch in its endosperm cells, but in this latter case there is a probability that the processes of ripening were not entirely completed when the seeds were fixed in absolute alcohol. The condition of the testa seemed to show that they were ripe, and the seeds were falling from the pods, but in *Scilla sibirica*, and in *Narcissus pseudo-narcissus*, the starch found in the cells when the seeds were discharged from the pods, disappeared later.

It is to be noticed that in general appearance of the walls four types of cells are to be found :—

1. Cells which are prismatic in shape, and whose walls are considerably thickened, but with the original cell membrane clearly marked. In these, canals between contiguous cells are frequent. Ex. Polygonatum.
2. Cells where much reserve cellulose is present, and the shape of the original cell is somewhat obscured. Canals are less frequent here. Ex. Tulipa.
3. Cells where very little reserve cellulose is present, and this is laid down regularly on the walls. The canals between the cells are frequent. Ex. Galtonia.
4. Cells where the thickening has been slight, and this mainly at the corners. Ex. Paris.

Reserve matters in the form of proteids and oil are everywhere associated with reserve cellulose in the cells. This kind of reserve is in inverse proportion to the amount of reserve cellulose. When much reserve cellulose, and consequently little other reserve, is present, the seeds are almost stone-hard when dry, and comparable with the ivory-nut, where mannose-yielding reserve cellulose was first discovered.

Only in exceptional cases is starch associated with these other reserve matters in the endosperm. This is true in Paris and Trillium, and, in both of these seeds, the reserve material on the walls is inconsiderable.

Interesting resemblances between the seeds of related genera are apparent, as well in the outward appearance as in the behavior toward microchemical tests. Paris and Trillium cited above illustrate this.

Of the twenty-eight genera studied these two are exceptions to the rule that in Liliaceae, Amaryllidaceae, and Iridaceae, reserve cellulose forms an important part of the nourishment stored in the seed for the young plant, and that starch is not present as a reserve matter.

It should be mentioned that the association of starch as a reserve with reserve cellulose in seeds of *Paris quadrifolia* was first pointed out by Reiss.[1]

MICROCHEMICAL BEHAVIOR OF RESERVE CELLULOSE.

Cellulose has been defined as a carbohydrate of the composition $(C_6H_{10}O_5)_n$, which is dissolved in cuprammonia, and is colored blue with chloroiodide of zinc, with iodine, and with sulphuric acid. It has, however, been found necessary to distinguish various modifications of cellulose occurring in the cell membranes of plants.

Ordinary cellulose of cotton-fibers and cell membranes of young roots have a certain well-known action in the presence of iodine solutions, acids, caustic alkalies, coloring fluids, etc. Lignified membranes, suberized walls, etc., present certain marked characteristics, which are none the less clear in the typical cases because gradations between classes appear.

It seems possible to define the behavior of the reserve cellulose, as found in the seeds of Liliaceae, in the presence of microchemical tests, even though certain minor differences appear in the different seeds.

Reserve materials of the cell wall have been divided by Tschirch[2] into two classes, cellulose and vegetable mucilage. These, he says, are closely related, gradations between the two being found. Under cellulose he names two forms, the first that of *Phoenix dactylifera* and *Phytelephas macrocarpa*, which he terms "reserve cellulose"[1]; the second that of Lupinus, Balsamina, Tamarindus, Paeonia, and Sabadilla, which he terms "amyloid," as other botanists[2] have done, the distinguishing mark being its behavior with iodine, in the presence of which reagent it turns blue, as starch does.

---

[1] Reiss, Ueber die natur der reservecellulose. Landw [illegible] jahrbücher, 18, s. 740.

[2] A. Tschirch, Angewandte [illegible] 1889.

Tschirch[1] considers that the reserve on the cell walls of the endosperm cells of Phoenix and Phytelephas is pure cellulose.

Reiss has shown that mannose-yielding reserve cellulose is present in *Paris quadrifolia* and *Foeniculum officinale* as well as Phoenix, Phytelephas, and a number of other seeds. On the other hand Paris and Foeniculum seeds are exceptional, in that reserve cellulose of the endosperm cells is not dissolved by cuprammonia.[3]

In the following experiments the material used, unless otherwise noted, is from dry, ripe seeds. Control tests were made with cotton-fibers, and young succulent shoots.

Behavior toward Weak Mineral Acids. The action with hot, weak, mineral acids is perhaps the most important, as it is universal. In order to determine the behavior of reserve cellulose with sulphuric acid, sections of seeds of *Polygonatum multiflorum* were boiled in one part concentrated sulphuric acid to five parts water. At the end of half a minute, the thickening on the walls had greatly swollen, and much had dissolved away, and after one minute the solution was complete; the primary membrane with haemotoxylin took the strong coloring of pure cellulose, and with iodine remained colorless. With *Asparagus officinalis*, the reserve cellulose was entirely dissolved from the cells in one half minute's action of the hot acid. The same was the case with *Allium cepa*, *Iris pseudacorus*, and others.

Sections of *Scilla sibirica* show swelling of the cell walls with one minute's treatment with hot acid, and in two minutes the solution is effected. The reserve from cells of Tulipa seeds is also a little more slowly dissolved than from Polygonatum, and shows, during the process, the gradual separation of the cells from one another, by the solution of intercellular substance. When iodine is applied, before the solution is complete, the bounding walls of the separating cells are yellow, whereas the intercellular masses are brown.

Pl. 2, fig. 1, shows a portion of the endosperm of *Polygonatum multiflorum* after one minute's boiling in sulphuric acid of the strength noted above. The reserve has disappeared from the cell walls, and the contents of the cells are not entirely removed. In fig. 2 the action of the acid has removed the cell contents as well.

---

[1] A. Tschirch, ibid, s. 171.

[2] Schleiden, Ueber das amyloid. Beiträge zur botanik, 1844. Frank, Journ. f. prakt. chemie, 1895, s. 479, etc.

[3] Reiss, Landwirthschaftliche jahrbücher, 18.

Pl. 2, fig. 3, exhibits a view of some cells from *Tulipa gesneriana* during the process of solution; the section was heated with iodine; the walls at *a* are yellowish; the masses of intercellular substance at *b* are brown.

The action in weak hydrochloric acid is similar to that with sulphuric.

Sections boiled in solutions of one part smoking acid to four of water lose the reserve of their walls in three minutes. Tulipa requires five minutes' boiling for the complete solution of the reserve from the walls. Sections from young stems of Primula, Begonia, Tropoeolum, and cotton-fibers were subjected to the action of acids of the above strengths, and serve to prove the different behavior of reserve cellulose towards these hot solutions of acids.

Acetic acid does not affect the reserve cellulose. Cold, weak, mineral acids act very slowly. Sections of Polygonatum after four days in sulphuric acid, of the strength which was used for the hot acid, were scarcely affected. At the end of twenty-four days in hydrochloric acid, one part acid to four of water, the walls of the endosperm cells in Polygonatum were much swollen, and, in some cases, the reserve was dissolved. *Allium cepa* sections were not much affected after nine days in hydrochloric acid. Pl. 2, figs. 4 and 5, illustrate the action of cold solutions of hydrochloric acid on Polygonatum. Concentrated sulphuric acid dissolves the reserve cellulose and the primary membrane very quickly.

Alkalies. The endosperm of Polygonatum seeds is not visibly affected by strong or weak alkalies; when sections of the seeds are boiled in a concentrated solution their walls swell slightly.

In Colchicum seeds, the endosperm is not noticeably affected by weak or strong, cold or hot caustic potash. The cell walls in the seeds of *Iris pseudacorus* swell slightly with cold, weak caustic potash, more with strong solutions, and the action is still more marked when these solutions are hot. *Scilla sibirica* has the walls of its endosperm cells strongly swollen in hot, strong caustic potash, though they swell only slightly in weak solutions. Sections of *Paris quadrifolia*, from seeds not quite ripe, were treated with hot, weak solutions of caustic potash and the thickenings were dissolved from the walls.

The action of caustic soda upon reserve cellulose is similar to that of caustic potash.

Solutions of Iodine. When the ripe endosperm of Polygonatum seeds is treated with iodine in potassium iodide, the thickened cell walls immediately take up the reagent in great quantities and become red-brown, or, when the iodine is supplied in sufficient quantities, almost black. This power of absorbing great amounts of iodine with the brown reaction is characteristic of the reserve material of the walls of the endosperm cells in Liliaceae, Amaryllidaceae, and Iridaceae. In only three cases are exceptions found, and in these the cell walls remain colorless after treatment with the iodine, or well-nigh so. These plants are *Paris quadrifolia*, *Trillium ovatum*, and *Colchicum autumnale.* The deep brown color, which, everywhere else in these endosperm cells, results from the iodine furnished, varies in shade to dull gray-brown, as in seeds of *Allium ursinum*, but clear red-brown is the general rule.

If iodine is supplied to the reserve cellulose in very small quantities, particularly if alcoholic solutions are weakened with water, or a crystal of iodine is dissolved with water on the slide, the cell walls are not uniform in their behavior in the different seeds.

Some are blue, or violet with tendencies to dirty brown; others are clear yellow or yellow-brown, with no tinge of violet or blue.

Asparagus officinalis, *Hosta caerulea*, *Ornithogalum caudatum*, *Narcissus pseudo-narcissus*, and *Lilium martagon* are yellow or yellow-brown with no tendency to violet or blue; this is also the case with *Allium cepa*, while *A. ursinum* is pale violet to dirty brown. All the other seeds show in their reserve a trace of violet or blue, when weak, watery solutions of iodine are applied.

In *Scilla sibirica* the color is often a clear beautiful blue, but it varies somewhat in different seeds.

To summarize: we notice the following reactions with iodine solutions.

1. With strong potassium iodide solutions.

a. (The exceptions.) Nearly colorless. Examples. Colchicum autumnale.
Paris quadrifolia.
Trillium ovatum.

b. (The rule.) Deep brown-red to gray-brown. Exs. Polygonatum multiflorum.
Iris pseudacorus.
Lilium martagon.
Lloydia serotina.
Galtonia candicans, etc.

2. With weak watery solutions from a crystal of iodine, or alcoholic solutions weakened with water.

a. Yellow, or yellow-brown. Exs. Asparagus officinalis.
Ornithogalum caudatum.
Hosta caerulea.
Narcissus pseudo-narcissus.
Lilium martagon.
Allium cepa.

b. Violet, or blue, or violet-brown. Exs. Iris pseudacorus.
Polygonatum multiflorum.
Galtonia candicans.
Allium ursinum.
Tulipa gesneriana.
Scilla sibirica.

Nägeli[1] groups together under the name amyloid, the carbohydrates which are colored indigo-blue or clear violet by water solutions of iodine, and considers that where a dirty violet or bluish brown color occurs, the substance is a transition form from amyloid to mesamylin, by which term he characterizes the cellulose of the membranes of plants, which is not colored at all, or only from yellowish to yellowish brown, with iodine. This transition form he has found in the seeds of *Iris güldenstedtiana* and in some species of Liliaceae and Amaryllidaceae. Amyloid, according to Reiss[2], is the constituent of the cell walls of plants, which is blue with iodine and does not yield mannose.

He finds mannose-yielding reserve cellulose in seeds of *Allium cepa*, *Asparagus officinalis*, *Iris pseudacorus*. In further characterizing the reserve he says, "Gegen *jodreagentien*, natronlauge, und Schulze'sches gemisch verhält sie sich ähnlich wie cellulose."

The three seeds mentioned above do not react with iodine in the manner of ordinary cellulose, and *Iris pseudacorus* shows a tendency to the blue color which characterizes amyloid.

Furthermore Reiss[3] remarks, "Es war daher zu erwarten, dass das für die [illegible] ermittelte, auch für die ganze familie der Liliaceen gelten möchte. Ich habe deshalb noch die samen von *Asparagus officinalis* verzuckert. Auch sie lieferten seminose. Nun ist Asparagus ein vertreter aus der unterfamilie der Smilaceen während Allium der Lilieen angehört. Es berichtigt dies also um so mehr zu der annahme dass allen Liliaceen mit verdicktem endosperm die gleiche form der reservecellulose eigen ist."

The natural conclusion from the above statements of Reiss would be that the reserve cellulose in all the seeds of Liliaceae would react the same in the presence of iodine. This is not found to be the case, as has been shown. On the other hand, I am inclined to think that here, in some cases, as Schulze[4] has found elsewhere, there is a combination of substances, which would yield by hydrolysis different sugars, side by side. Probably in all, the ground substance is the same, but it is difficult to suppose that the blue color of *Scilla sibirica* in the presence of iodine is produced by exactly the same substance which in other seeds is colorless or brown.

---

[1] C. Nägeli, Die chemische zusammensetzung der stärkekörner, s. 209-210. 1855.

[2] Reiss, Landw. jahrbucher, 18, s. 763.

[3] [illegible]

[4] [illegible]

Iodine and Sulphuric Acid. If we treat the endosperm cells of *Polygonatum multiflorum* with iodine, and then with sulphuric acid (one part water, with two parts sulphuric acid), the usual cellulose reaction is confined to the primary membrane and the reserve material is turned deep violet-blue, quite different from that of cellulose, while it swells and dissolves slowly. Tulipa shows no sign of blue coloring with iodine and sulphuric acid, having instead a red-brown color, and it does not dissolve after half an hour. Asparagus does not give the violet-blue with this treatment that Polygonatum does. *Allium cepa*, *Iris pseudacorus*, and others show the same reaction as Polygonatum with iodine and sulphuric acid.

Chloroiodide of Zinc. Chloroiodide of zinc acts upon the reserve cellulose in the same way as iodine in solutions of potassium iodide does. All the seeds studied show a brown color in the reserve of the endosperm walls except Paris and Colchicum, which react the same as with iodine. In the crest cells of the seed of Colchicum, which before the ripening of the seed are filled with starch, the cellulose reaction with chloroiodide of zinc takes place, and the blue color appears.

Cuprammonia. With this reagent the reserve cellulose is entirely dissolved from the endosperm of all the seeds examined, with the exception of *Paris quadrifolia.*[1] In Polygonatum, the reserve cellulose was dissolved in ten minutes. *Iris pseudacorus* had the walls dissolved in twenty minutes. Tulipa, Scilla, Colchicum, Ornithogalum, Allium, and Narcissus range between these two in the time required to complete the solution of the walls of the endosperm.

Anilin Sulphate and Phloroglucin with Hydrochloric Acid. These reagents do not affect reserve cellulose.

Phloroglucin and hot Hydrochloric Acid.[2] On the possibility of finding that reserve cellulose would give the rose-red reaction of the pentaglucoses, when treated with these reagents, sections of Polygonatum, etc., were treated with an alcoholic solution of phloroglucin until they were impregnated with it, a little water was added and the sections were then heated in hydrochloric acid, but in no case did the endosperm yield the rose color.

Action of Boiling Water. When sections of Polygonatum seeds are boiled in water for 6–9 hours, the structure of the cell wall is apparently unaltered. This is true of the seeds of Colchicum, Scilla, and Tulipa. These react, too, in the same way toward iodine as before boiling. *Iris pseudacorus* showed the walls of the endosperm very much swollen after eight hours' boiling.

---

[1] Reiss, Landw. jahrbücher, 18, s. 711.

[2] Schulze, Ber. der deut. chem. gesellschaft, 24, s. 2279.

In sections of Paris seeds which were not quite ripe, the endosperm cells had their thickened corners much swollen after eight hours' boiling.

Pl. 2, fig. 6, is a sketch of a few cells from the endosperm of Polygonatum, after eight hours' boiling; the contents of the cells have been boiled away, but the reserve is unaffected on the walls. The section was tangential to the seed, and the canals between the contiguous cells do not, on that account, always correspond; at *a* the surface of the cell wall shows, with the ends of the canals appearing as pits.

Pl. 2, fig. 7, represents the appearance of the cell walls of the endosperm of *Iris pseudacorus* after eight hours' boiling; *a* distorted wall, *b* contents of the cell. This should be compared with Pl. 1, fig. 2, which shows the cells of *Iris pseudacorus* treated with iodine.

Pl. 1, fig. 9, shows the swelling of the reserve material in the endosperm walls of *Paris quadrifolia*, when allowed to lie in water some time. The seed was not quite ripe.

Pl. 1, fig. 8, is a sketch from the seed of *Paris quadrifolia* treated with absolute alcohol.

Action with Staining Fluids. Haematoxylin stains the reserve cellulose of Polygonatum seeds but slightly; the primary membrane, however, shows a beautiful deep violet color, which perfectly outlines the original cell walls.

This is the case with seeds of Ornithogalum, Iris, Asparagus, etc. Tulipa takes the stain most vividly on the inner surface of the cells, for the reserve cellulose seems to be laid down as intercellular substance, as its method of solution under the action of sulphuric acid has already suggested (see Pl. 2, fig. 3).

Methyl violet also brings out distinctly the original wall of the cell as a well-defined line in the midst of the faintly stained reserve material.

Congo-red, if applied to the sections for only a short time, from fifteen minutes to half an hour, is easily washed out with water, except from the primary membrane. If the sections are left in congo-red from twenty-four to forty-eight hours and then carefully washed, the reserve material is deeply stained. This color will hold perfectly for three months in seventy per cent alcohol.

Summary. As a result of the foregoing investigations the following statements may be made with regard to the characteristics of reserve cellulose as seen in the Liliaceae.

1. Its easy solubility with hot, weak, mineral acids; the hemicellulose of Schulze.

2. Its deep brown color with iodine in potassium iodide, with the exception of Paris, Trillium, and Colchicum seeds.

3. Its behavior toward chloroiodide of zinc as toward iodine in potassium iodide solutions.

4. Its resistance to the action of boiling water; exception, *Iris pseudacorus* and unripe seeds of Paris.

5. The slight coloring with haematoxylin and methyl violet.

6. Intense coloring after long exposure to congo-red.

7. Violet-blue in many cases with sulphuric acid after iodine.

In the above particulars, it is to be distinguished from ordinary cellulose.

8. The solubility in cuprammonia.

9. Behavior towards caustic alkalies.

These last two characteristics it shares with ordinary cellulose, as in cotton-fibers, young shoots, etc. In general the reaction of the reserve cellulose in the presence of microchemical tests is fairly uniform, but there are some exceptions.

The most noticeable of these are: —

1. The reactions with weak, watery solutions of iodine, where the range is from blue and violet to brown, or the walls remain colorless.

2. The swelling of the walls of the endosperm cells of *Iris pseudacorus* and Paris with boiling water.

3. The exceptions to the action of sulphuric acid after iodine, as in Tulipa.

4. The different lengths of time required to dissolve the reserve cellulose in the presence of weak acids and cuprammonia.

5. The reserve of Paris is exceptional in the following particulars : —
    a. It swells considerably with water.
    b. It does not dissolve in cuprammonia.
    c. It is colorless with iodine, while Colchicum is faintly yellow.
    d. It occurs in connection with starch as a reserve substance.

Trillium ovatum agrees with Paris in the three particulars investigated, and it is probable that it will be found insoluble in cuprammonia.

These facts seem to point to the following conclusions, with regard to reserve cellulose in Liliaceae.

1. That reserve cellulose is not identical with pure cellulose.

2. That it probably consists of a ground substance of [illegible] chemical nature in all the seeds; Paris and Trillium may be exceptions.

3. That the slight differences, noticed in the behavior of reserve cellulose, are due to the association of other substances with this ground substance in the same wall.

RESERVE CELLULOSE DURING GERMINATION.

In order to study the history and final fate of reserve cellulose, seeds were planted and examined during the various phases of germination, until the young plants no longer depended upon the seed for nourishment.

Sachs[1], as early as 1862, showed that reserve cellulose is a true reserve material, and is used up during the processes of germination. The seeds he studied were *Allium cepa* and *Phoenix dactylifera*. Reiss[2] has proved the same to be true of the reserve cellulose of many other seeds, both dicotyledons and monocotyledons; and he has given particular attention to the mechanical process of solution. Furthermore, he has proved, macrochemically, that many seeds containing reserve cellulose, among them *Iris pseudacorus* and *Allium cepa*, yield mannose by hydrolysis.

It is of interest to follow under the microscope, so far as the limited development of microchemistry will allow, the chemical result of solution.

The following sketches of the history of the germination of the seeds of *Polygonatum multiflorum*, *Iris pseudacorus*, etc., will illustrate the changes of the reserve cellulose during solution and absorption.

Germination of Seeds of Polygonatum multiflorum.

Seeds of *Polygonatum multiflorum*, gathered Sept. 11, 1892, were planted April 24, 1894, after three days' soaking in water.

After eight weeks, on June 19, they were found to have sprouted. The manner of germination is peculiar. The first effort of the plant is to establish itself firmly in the soil, and, to this end, it begins at once the construction of the rhizome which is so characteristic of the genus.

The seed is spherical and hard, containing a large endosperm consisting of good-sized cells, whose walls are considerably thickened with reserve cellulose. In the cells are present oil and reserve protein matters, but no sugar and no starch. (Plate 1, fig. 1, illustrates these cells.) The embryo is small (Pl. 3, fig. 1), and consists of a cotyledon, sheathing the vegetative point ; and of a minute hypocotyl. When a section is made through a seed which has been lying sometime in the soil, but has not yet protruded its radicle, the embryo is seen to be in quite an undeveloped state and no growth has taken place. In section, the embryo is slightly spoon-shaped, consisting almost entirely of the cotyledon which, at its base, sheaths the vegetative cone of the future upward axis. Below this is the tiny hypocotyl bearing a well-developed root-sheath.

---

[1] Sachs, Keimungsgeschichte der Allium cepa etc. Bot. zeit., 1862–63.

[2] Reiss, [illegible]

The vascular system is outlined in both cotyledon and hypocotyl by nascent tissue.

The root-cap is strongly marked by the presence of starch, which has appeared in its cells since the seed was put in the ground.

Starch-builders are detected below the vegetative cone and in the cotyledon. Plate 3, fig. 2, shows at A a section of the embryo before growth has taken place ; *a*, cotyledon ; *b*, hypocotyl ; *c*, vegetative cone ; *d*, nascent vascular tissue ; *e*, root-cap. Plate 3, fig. 2, shows at B the region of vegetative cone, more enlarged ; *d*, cotyledon ; *b*, nascent vascular tissue ; *c*, vegetative cone ; *a*, cells containing starch-formers.

The cells of the cotyledon contain a good deal of oil in small globules, particularly at the apex and in the outer layer of cells, which are in contact with the endosperm. Much of this oil, probably all, has been stored up in the cotyledon cells themselves and was not withdrawn from the cells of the endosperm. When aggregated by treatment with chloral hydrate, and stained with osmic acid, the oil presents the appearance seen in Plate 3, fig. 2, C.

When the oil is removed by absolute alcohol, the starch-formers show more clearly, and the presence of minute grains of starch in them can be demonstrated by warming the slide after the iodine has been applied. Pl. 3, fig. 2, D, shows a few cells from below the vegetative point, which have been treated with absolute alcohol and iodine ; the starch-formers are apparent.

Outside the cotyledon, in contact with the endosperm cells, but not in them, are a few oil drops.

With congo-red the cells of the endosperm take the characteristic reaction of reserve cellulose, coloring with some difficulty but strongly. The cells of the cotyledon show a bluish tendency with congo-red, indicative of the presence of acid in small quantities. With iodine, no difference is detected between the reserve cellulose in this stage, and the resting winter state.

The only changes, since water was furnished the seed and germination started, are the softening and swelling of the tissues; the possible withdrawal of a small amount of oil from the endosperm cells; and the development of starch in the embryo.

The examination of a young seedling still buried in the ground exhibits a long vigorous root and a short, considerably thickened stem whose cells are gorged with starch. In this we see the beginning of the formation of the rhizome. The small bud has broken away from the sheathing petiole of the cotyledon, but is still little developed. A part of the cotyledon remains in the seed, and has enlarged to half the capacity of the seed, replacing the endosperm. Its petiole grew just enough to carry the hypocotyl and bud out of the seed and then enlarged.

Pl. 3, fig. 3, A, is a view of a young seedling in section, and B is the same enlarged. The section has been treated with iodine; *a*, undissolved reserve material of the endosperm to which iodine imparts the characteristic red-brown color; *b*, endosperm cells, from which reserve material has been dissolved and which are unstained with iodine; *c*, the cotyledon with its vascular system well formed; *d*, portion of the cotyledon which carried the bud out of the seed; *e*, bud which has freed itself from the sheathing cotyledon; *f*, the stem already thickened and containing starch, *i. e.* the young rhizome; *g*, root-hairs. Comparison with fig. 4, a younger stage of the seedling, will show the manner of extricating the bud from the seed. In this case the cotyledon is curiously lobed, and the sheath is apparent.

In cotyledons from seedlings of this stage of development, there are short, well-formed spiral vessels in the vascular portions, and the system in the stem and root is well developed.

The cells which lie in contact with the endosperm contain much oil — a little is to be found in cells in the neighborhood of the vascular portions, but none is to be found in the portions of the seedling which lie outside the seed.

Starch-formers are to be found in the cells, near the bounding layer of the cotyledon and near the vessels, and in these minute starch grains may often be detected. The presence of starch in the cotyledon is not constant; sometimes the cells contain considerable quantities, but always in minute grains.

The thickened stem and apical bud contain starch in grains, which seem permanent.

In general the cells of the cotyledon in the seed are rather empty. No sugar is found in the seed, but in the cotyledon outside the seed a little is detected.

In the endosperm, important changes have taken place. The outer masses next the seed-coats still take the characteristic red-brown color, and are unchanged. Adjacent to these, lie cells whose walls are no longer thickened, and remain colorless under the action of iodine; and farther in, in contact with the cotyledon, are mere shreds of pressed and distorted cell walls.

In Pl. 3, fig. 5, A, the condition of the endosperm cells which lie next the cotyledon is seen. Relics of former endosperm cells which have been exhausted of their contents, and pressed upon by the growing cotyledon *c*, appear at *f*; and at *g*, are loose cells, which are empty but for the large oil drops.

In B at *a*, are cells which have been distorted by pressure.

The contents of the cells, as well as the reserve of the walls, are gradually withdrawn during the encroaching growth of the cotyledon.

The solution of the reserve from the walls is slow and irregular; sometimes the thickening remains at the corners after the rest of the walls are freed; sometimes one wall is affected before the others; and sometimes a large number of cells show a gradual melting away of the substance toward one direction. In the latter case the regular thinning of the walls produces a gradual shading of the color which iodine gives. In Pl. 3, fig. 7, an attempt has been made to represent, by light and shade, the appearance of the reserve cellulose, during its gradual withdrawal from the walls.

Pl. 3, fig. 6, illustrates the more irregular solution of the substance. While the solution is going on in the cells, the nucleus often lies in contact with the walls, and these cells, which already have given up their reserve protein matters, contain vacuoles and streaming protoplasm. Granular masses, filled with minute oil globules, cling to the dissolving walls. No starch is visible in the endosperm at any time and only a trace of sugar, if any, is to be detected. Pl. 3, fig. 6, is a characteristic sketch, showing the oily, granular masses in contact with the walls, which are losing their reserve material; at *n*, is the nucleus.

A section, which shows the outer layers of the cotyledon and several layers of the endosperm cells, exhibits the phases of solution and absorption.

First, the thickly-filled endosperm cells give up their protein reserve matters and, probably, some oil; then the cells, with the protoplasm in an active state and with large vacuoles, begin to lose the reserve masses of the walls; and, lastly, the protoplasm and the oily matters, which seem to be derived, largely, from the cell walls themselves, are withdrawn, and, pressed upon by the cotyledon, the cells collapse. In the cotyledon, on the other hand, appear masses of oil in the outer layer of cells. None is found in the plant outside the seed, and only a little in other cells of the cotyledon. Instead, starch is formed in the starch-formers in the cotyledons in small, but varying amounts, and in large, and more permanent masses, in the bud and young rhizome.

Pl. 3, figs. 6 and 7, show the contents of the cells during the solution and withdrawal of the nourishment from the endosperm. In fig. 7, 1, are cells of the cotyledon, with abundant oil in the outer layer; at *n*, the nucleus; at *g*, in the second layer appear the starch-builders. At 2 are the walls of the collapsed cells pressed upon by the growing cotyledon. At 3 the cells are nearly empty, and all the reserve cellulose is [illegible]. At 4 there is some reserve cellulose, which is gradually being removed; the cells still contain oil and protein matters. The outermost cells have been scarcely affected.

This process, which has been outlined, goes on until all the nourishment has been absorbed from the endosperm, the cotyledon acting as agent of absorption and transfer. The visible chain of processes is reserve cellulose, then oil in the endosperm; and in the cotyledon, oil and starch. In the young plant the supplied material is used up and growth ensues.

If sugar is formed, and traces of it are certainly to be found in the cotyledon, it is carried over at once into some other compound.

Germination of Iris pseudacorus.

Seeds of *Iris pseudacorus*, which were gathered Oct. 1, 1892, were soaked four days and on April 28, 1894, were planted. After 20 days, on May 18, they had appeared above the soil, the largest being then three fourths of an inch high. The examination of the unsprouted seed shows, as in Polygonatum, a minute embryo imbedded in endosperm, whose cells are hard and firm, the walls being encrusted with reserve cellulose. Through the imbibition of water, the cell walls are slightly swollen and the tissue softened. No other change has taken place since the seed was placed in the ground. The embryo consists of a sheathing cotyledon, which encloses the young bud, and of a minute hypocotyl.

The method of growth is as follows. The growth of the sheathing petiole of the cotyledon carries the hypocotyl and enclosed bud out of the seed. The root grows vigorously downward, and the hypocotylary stem upward, to carry the protected bud above the soil. At the same time, the stem of the cotyledon keeps pace with this growth so that the seed may not be carried up as well. A sharp bend is made by the petiole of the cotyledon, like an elbow joint; one part reaches down to the seed, the other, serving as protection for the bud, is united below to the stem. The upward growth of the stem and that part of the cotyledon next it, always corresponds to the growth of the other arm, which reaches to the seed, so that the seed always remains in the soil at the level of the neck of the root, and the elbow becoming hard and horny serves to make a way through the soil. When above the ground, the sharply-pointed end of the first leaf cuts through the sheath.

Pl. 4, fig. 1, A, shows a young plant of *Iris pseudacorus*, twenty-five days after the sowing of the seed; *a*, seed with thick testa; *b*, petiole of the cotyledon; *c*, horny tip of the same; *d*, sheathing portion of the same; *e*, hypocotylary stem; *f*, root; *g*, first leaf. B, section of the seed of the same plant, with testa removed; *a*, cotyledon; *b*, endosperm; *c*, the same with reserve dissolved from the walls. The cotyledon acts in four ways: to extricate the embryo from the seed; to protect the young bud; to break through the soil; and to supply the young plant with nourishment. The source of nourishment is the endosperm of the seed. An examination of a young seedling is interesting. Pl. 4, fig. 2, is instructive; it exhibits a section of the seedling, treated with iodine. The endosperm has for the most part the characteristic red-brown color, but near the cotyledon the cells are colorless, showing that reserve cellulose is no longer present. The flat spoon-shaped tip of the cotyledon has enlarged somewhat and is filled with starch. The young stem and bud, as well as the sheathing part of the petiole, contain starch.

In fig. 3, a section of a seed from a plant three inches high is illustrated; the process of solution has gone still farther and nearly all the reserve material of the endosperm is exhausted. Irregularly arranged around the edge of the seed, cells can be seen whose walls are still thickened with reserve. The solution has left the cells intact, but they are easily separated from each other in the cutting of the sections. The cotyledon does not grow as does that of the Polygonatum, crowding the exhausted cells together in the endeavor to reach the material stored in the outermost layers. The method is different.

At a certain stage of development, when the vascular system is well formed, the cotyledon in the seed ceases to grow, and the cells of the endosperm themselves act as carriers of the material, which the cotyledon needs, from the distant cells, which are still capable of furnishing it.

These intermediate cells remain healthy; they are filled with protoplasm, which shows its activity by the rate and vigor of its streaming, and this goes on for some time, even after the cells are isolated from one another. They contain much oil in small globules, and granular matters appear in the protoplasm.

Pl. 4, fig 4, shows an isolated cell from which the reserve cellulose is dissolved. Its walls are clear and colorless with iodine. Streams of protoplasm run in every direction, and much oily matter lies in the masses next the walls. At *a* a large oil drop is breaking up into tiny globules, which are swept in the current of protoplasm toward the wall. The oil in these cells is colored only slightly by iodine, whereas osmic acid stains it brown or black. Fehling's solution fails to detect more than the merest traces of sugar. The cells are much freer of protein reserve matters than during the resting winter stage, and large vacuoles are present.

Their appearance in this particular is in strong contrast to those cells nearer the edges of the seed, which are not yet affected by solution, as well as in contrast to their own earlier state.

Instead of being gorged with reserve both on the walls in the shape of reserve cellulose, and in the cells in the shape of oil and reserve proteids, the cells are thin-walled and contain actively streaming protoplasm, the other matters being in a finely divided state. Compare Pl. 1, fig. 2, with Pl. 4, fig. 4. Here the cells are active agents of solution and transfer instead of being passive receptacles.

In close contact with these vigorous cells are those of the outer layer of the cotyledon, which contain protein matters in abundance, and oil of a different nature from that found in the endosperm, for with iodine it colors red-brown. The cells deeper in the cotyledon contain much starch, as well as those in the neighborhood of the vessels.

When the section is subjected to the influence of methyl violet and haematoxylin, the reserve material takes up the color but little, whereas the cells whose walls are freed from the reserve act as ordinary cellulose. When sections of the seed are placed in congo-red for half an hour, the color is taken up in quantities by those cells with no reserve; and little is taken up by the thick walls, which, as yet, are not affected by solution. When, on the contrary, the congo-red is allowed to act for twelve hours, the reserve is more deeply stained than those cells which contain none. This harmonizes with the action observed in the dry seed, when comparison is made with true cellulose.

With the longer or shorter action of congo-red, the cells of the cotyledon turn slightly bluish, probably showing the presence of acid in small quantities, to which congo-red is very sensitive.

To summarize: nourishment is furnished the young plant by the cotyledon; the source of the nourishment is the material stored in the endosperm, *i. e.*, reserve cellulose from the walls and protein matters from the cells, together with some oil.

The endosperm first gives up the reserve proteids and oil, next the reserve cellulose, which is in part, at least, visible in the cells in the shape of minute oily globules.

This reappears as oil in the outer layer of cells of the cotyledon, but the end product is starch, which is found in the cotyledon and in the growing parts of the seedling. The endosperm cells act with the cotyledon as agents in the chemical and mechanical process of solution and transfer.

Iris sibirica presents, during germination, the same phenomena as *Iris pseudacorus.*

Germination of Allium cepa.

Seeds of 1893 of *Allium cepa* were sown, April 24, 1894, and on April 28, germination had begun.

Sachs[1] has shown that the thickening on the walls of the endosperm cells in the seeds of this plant disappears during germination. Pl. 1, fig. 5, I, II, and III.

---

[1] Sachs, Keimungsgeschichte der Allium cepa, etc. Bot. [illegible]

shows the habit of the young plant during germination; *a*, seed brought above ground; *b*, cotyledon; *e*, root.

The cotyledon is here somewhat coiled, as it lies in the endosperm. During growth the reserve cellulose is dissolved away from the walls, leaving them almost isolated, but active. The method of withdrawing nourishment from the cells is much as in Iris, for the cotyledon does not enlarge so as to fill the seed as in Polygonatum.

The endosperm cells retain their protoplasmic contents and act as transfer agents from the cells beyond them. Pl. 4, fig. 6, shows a seed of *Allium cepa* in section, when the reserve is almost entirely exhausted, a little only remaining on the walls of the cells in the neighborhood of the micropyle, at *c* in the figure.

All the cells contain protoplasm and oil, and the greater number have large vacuoles, the granular protein matters having been withdrawn. This seems to be the first action of the cells.

The coiled cotyledon contains a great deal of oil in all the cells, and no starch, in these respects differing from Polygonatum and Iris. Starch is found exceptionally in the cotyledon, when the growth has been stunted by accident, as when the root-tip was broken off, or occasionally, when the plant has well established itself and is assimilating vigorously before the reserve material is all exhausted. In other words: starch is sometimes formed when the transfer of food to the young plant is checked. A little sugar appears in the endosperm and in the cotyledon, but, as in the other seedlings, in very small amounts. Pl. 4, figs. 7 and 8, illustrate the method of solution of the reserve from the walls.

Summary. From the study of the germination of *Polygonatum multiflorum*, Iris, and Allium, we gain a general idea of the history of the reserve cellulose during germination.

1. The method of solution, in all the seeds, points to the fact, elsewhere proved, that the reserve cellulose has been laid down on the original cell walls as a secondary product, not as a constituent part of the original wall.
2. The solution goes on, while the protoplasm of the cell is in an active state.
3. In all cases where the solution is going on, minute globules of oil are found in close contact with the wall. These are of a kind not colored, or only slightly so, with iodine.
4. Oil is transferred to the cotyledon, and is found either in the outer layers of cells, as in Polygonatum and Iris, or throughout the mass of the cells, as in Allium.
5. Starch is only an end product of this activity and does not appear at all in the cotyledon of Allium unless the removal of material is arrested.
6. Sugar can only be detected in minute quantities during these processes.

7. In all the seeds the cotyledon is the agent of absorption [illegible]. In Allium and Iris, a large number of the endosperm cells are also active in transferring the reserve material, and in these cases, all the cells contain protoplasm and oil until the reserve cellulose is exhausted, and then, only, become empty and collapse.

DEVELOPMENT OF RESERVE CELLULOSE IN THE SEED.

To understand rightly the nature of the reserve cellulose, regard must be had to the phenomena connected with its appearance during the formation of the seed. Accordingly, fruit-pods of *Iris sibirica*, and berries of *Polygonatum multiflorum*, have been gathered during the formation of the seed, and all the different stages of development have been followed under the microscope. These observations have been combined with a less detailed study of a number of other seeds, during the processes of ripening, so that a somewhat full history of the origin and growth of reserve cellulose in the Liliaceae, and its allies, lies before us.

Growth of the Seed of Iris sibirica.

Iris sibirica, on June 20, 1891, four weeks after flowering, had well-developed fruit pods, with young seeds, which, in many cases, contained well-formed embryos, and endosperm, in which cell division had ceased and the walls were formed.

The young seeds are flat and green, the immature testa containing much chlorophyll.

Next these loose cells of the outer integument lies a layer of firm, small cells, with no intercellular spaces. Each of the cells in the layer contains a large greenish yellow, oily globule, which half fills it. Two layers of spongy, almost empty, cells lie between these and the endosperm.

The endosperm cells, when cell-division has ceased, show, in sections made in the plane of the long diameter of the seed, a radical arrangement. The small, though perfectly formed, embryo lies at the micropylar end, and opposite, as the ovule is anatropous, the firm irregular cells of the chalaza appear, to which leads the bundle of spiral vessels, which furnishes the path of food communication with the mother plant.

Pl. 5, fig. 1, presents a view of a section of the seed, taken in the plane of its long diameter at this stage of development: *a*, endosperm; *b*, embryo; *c*, layer of cells containing oil drops; *d*, chalaza, in whose cells is a little starch; *e*, chlorophyll, containing cells of the integument. Though the cells of the endosperm are all formed, the walls are very thin, and the protoplasm streams in delicate threads from the large nuclei to the walls. The protoplasm, in the masses, which are in contact with the walls, is very granular and contains many tiny oil globules.

The cells in general contain large quantities of oil and much sugar.

Pl. 5, fig. 2, is a sketch of a few of the endosperm cells cut in the plane of their long axes; the oil has been removed by absolute alcohol ; at *n*, is the nucleus.

The layer of small, close-set cells of the integument, which contain the greenish oil drops, is illustrated in Pl. 5, fig. 3.

The oil in these cells reacts differently toward osmic acid from that of the endosperm, the resulting color with this reagent being deep red-brown, not the ordinary black-brown.

Absolute alcohol dissolves it completely but more slowly than it does that of the endosperm. Much tannin is present in the integuments, as is shown by the reactions with ferric chloride, potassium bichromate, and osmic acid.

Sugar is also present, and at the chalaza a little starch occurs, outside the endosperm.

On July 10, ten days later, the thickening of the walls had begun in parts of the seed which were near the chalaza, and extended toward the center of the seed. The corners of the cells are first affected, and later the rest of the walls, these being thickened on all sides at the same time, and uniformly.

The cells contain much oil and granular matters and some sugar, though the reduction of Fehling's solution does not give so great a precipitate as in the earlier stages. Pl. 5, fig. 4, shows cells of the endosperm at the stage when the thickenings have only just appeared at the corners; the section was examined in absolute alcohol, and most of the oil had been removed. In the outer layers of the endosperm, where the walls are not thickened, the protein matters about the nucleus and the nucleus itself are stained red-brown in the presence of iodine. In these cells are peculiar crescent-shaped bodies, which also stain red-brown with iodine ; the nature of these bodies is not yet clear. Pl. 5, fig. 5, is a sketch of cells where they occur ; at *n*, the nucleus ; the section has been in absolute alcohol.

When the reserve cellulose appears in the endosperm, it is clear and colorless, and is not to be distinguished from the original wall until water is applied, then it begins to swell and, immediately, through the absorption of water, goes over into a jelly-like, mucilaginous modification, and the cell contents are pressed together into the middle of the cell. This process of swelling in the reserve cellulose can be easily followed, when to sections of the seed, which have been in absolute alcohol, water is added, for it is then, of course, much slower. The swelling at the corners of the cells begins immediately upon the addition of water and goes on until the structure of the endosperm is no longer visible, and a jelly-like mass containing distorted and disintegrated bits of cell-contents is all that can be seen.

When congo-red in water solution is added to fresh cut sections, the process is even clearer, for the forming jelly is colored irregularly through the mass, and, on the edges of the section, the rapid flowing out of the reserve cellulose from the cells in irregular masses can be traced.

If water with iodine is applied to fresh sections, the mucilaginous mass becomes slowly and evenly colored brown. Pl. 5, figs. 6 and 7, show stages in the swelling of the reserve cellulose; they are from the same section that is represented in fig. 4, after water is applied; later, only a jelly-like mass was to be seen. Chloroiodide of zinc produces a sudden, convulsive swelling of reserve cellulose, the protoplasmic contents of cells is pressed into the center, but connection is still preserved with the primary membranes on the five walls, at the points where least pressure from the swollen corners is felt; that is, in the middle of each wall. This produces a queer star-shaped mass in each cell, the arms of the stars corresponding with each other in the contiguous cells. Pl. 5, fig. 8, illustrates the curious effect produced upon the cells by this reagent; the swollen masses are not colored. Pl. 5, fig. 9, is a sketch of a section, cut in the other direction, also treated with chloroiodide of zinc.

The greenish oily globules in the cells of the integument have considerably increased in size, since the thickening of the endosperm cells began; they nearly fill the cells. Pl. 5, fig. 10, is a sketch of a few of these cells.

Seeds a few days older than those last described show that the walls, as well as the corners, have been thickened, so that the places, where the canals will appear, are already apparent. The outlines of the walls are smooth, and the thickening is regular. Pl. 5, fig. 11, shows the condition of the walls at this stage. With water, the peculiarities already noted in the earlier stages appear, the same mucilaginous modification resulting from its application. The contents of the cells are the same, except that the amount of sugar seems to be decreasing. No starch occurs in the seed; the little which in an earlier stage appeared near the chalaza, outside the seed, has disappeared.

To summarize: 1. Reserve cellulose appears in the cells of the endosperm soon after the cell-division has ceased.

2. Its appearance is preceded by a large amount of sugar in the endosperm, which lessens during the process of cell wall thickening.

3. Much oil appears associated with the sugar in the cells before the walls begin to thicken and is always present in the later stages.

4. The thickening of the walls is at first local in the cells between the chalaza and the center of the seed.

5. The process of thickening is gradual, the corners of the cells being affected before the rest of the walls.

6. Reserve cellulose in Iris is, while forming, easily affected by water, swelling, losing its structure, and becoming a mucilaginous mass.

7. This structureless mass is colored brown with iodine in potassium iodide.

8. Before the process of thickening has reached the cells of the outer layers of the endosperm, these cells contain proteids and crescent-shaped bodies, which are colored deep red-brown with iodine.

9. A close layer of cells containing oil with some layers of spongy cells forms the inner integument which encloses the endosperm.

Growth of the Seed of Polygonatum multiflorum.

The behavior of the reserve cellulose in seeds of *Polygonatum multiflorum* is in some particulars different from that in seeds of *Iris sibirica.* On July 1, 1894, the endosperm in many of the seeds of this species was completely formed, but the cell walls were still unthickened. Pl. 6, fig. 2, illustrates this stage, though the sketch was made from material (preserved in absolute alcohol and sulphur dioxide) which had been collected at a later date, in another season. The nucleus is at *n*. It lies near the center of the cells, contains several nucleoli, and from it threads of protoplasm reach toward the walls in every direction. Pl. 6, fig. 1, represents a few cells of the endosperm during the formation of the cell wall.

When the endosperm cells are formed, they contain sugar in large amounts, as do the cells of the integuments and the fleshy portions of the young berry. Much oil is present in the endosperm, but not so much as in corresponding stages of Iris. Pl. 6, fig. 3, shows a cell from material gathered, July 1, 1894; the oil has been aggregated with chloral hydrate; *n*, nucleus; *o*, oil.

The integuments do not contain so much tannin as those of Iris, and the oil-bearing layer is not present. Sugar is present in the integuments and fleshy placentae, but no starch is contained in the berry.

A later stage of the seed shows starch-formers in a few cells of the endosperm near the chalaza, and a few minute grains of starch are with difficulty detected. The walls of the cells are coated with a layer of protoplasm, which contains small oily globules. See Pl. 6, fig. 4, *n*, nucleus, with starch grains in the neighborhood.

Twelve days later, the thickenings of the walls had begun in the endosperm; this was in a V-shaped mass near the chalaza, with the apex toward the center of the seed.

The thickening is first at the corners of the cells, as in I[illegible] protein cases in contact with the walls, imbedded in protoplasm, which [illegible] and granular matters. Pl. 6, fig. 5, is a sketch of the endosperm at this stage of development; *n*, nucleus; *a*, thickened corners.

The addition of water does not cause any noticeable swelling in the reserve cellulose, but chloral hydrate does. Iodine stains the reserve cellulose the characteristic brown from the first. When the thickening has proceeded farther, the cell walls present the appearance seen in Pl. 6, fig. 6, which is from a different part of the section from which fig. 5 was made. The reserve cellulose is laid down regularly and evenly on the walls, and the canals are already visible.

In the layer of cells which bounds the circumference of the endosperm, no thickening of the wall has taken place. In these cells are starch-builders, and a few minute grains of starch; the protein matters become quite red-brown, when iodine is added. In the presence of minute grains of starch in the starch-builders the seeds differ from Iris, as in two other particulars; *i. e.*, the absence of the power of swelling with water, which the reserve shows, and the absence as well of the close-set cells, containing oil, which are found in the integument.

No starch appears later in the process of maturing of the seed in any of the cells of the endosperm

The thickening of the walls continues regularly, always associated with an abundance of oil in the cells.

Notes on other seeds.

Asparagus officinalis. Seeds of this plant on July 15 were still very young, and the endosperm was not entirely filled out, but the cells formed contained sugar, though no oil.

Somewhat later, oil appeared in the seeds in considerable amounts. Before any thickening of the walls took place, starch-builders with minute starch grains appeared in the cells between the chalaza and the center of the seed. In later stages as in Polygonatum this disappeared, and no more was formed as the seed ripened.

Paris quadrifolia of May 18 contained abundant masses of starch in the integuments of the seed, though the endosperm cells had only just completed the cell-building. Later, starch appears in the cells of the endosperm. Seeds, not quite ripe, show a swelling of the reserve cellulose, when water is added, though it is never carried so far that the structure is lost. Compare Pl. 1, figs. 8 and 9, which show cells of Paris with and without water.

Scilla sibirica, *Narcissus pseudo-narcissus*, and *Galanthus nivalis* contain starch in the endosperm cells, just before the processes of ripening are complete. Even when Scilla and Narcissus seeds have fallen from the pods this is the case, though in these seeds none is present during the winter resting-state. In these seeds only a trace of sugar is to be found in the later stages of ripening, and it finally disappears entirely.

Pl. 6, fig. 7, shows some cells of *Galanthus nivalis*, when only the cells in the center of the seed remain unthickened. The gradations are seen between these unthickened cells of the center, and the almost completed thickening of those nearer the integuments. At B the surface of several cells is shown, to illustrate the uneven distribution of the thickening on the walls; *s*, starch ; *n*, nucleus ; *a*, ends of the canals.

Colchicum autumnale of June 18, 1894, had apparently formed its reserve cellulose, but was not quite ripe. Oil, granular protein matters, and a little sugar were found in the cells of the endosperm. The large crest of the seed was full of starch, though none appeared in the endosperm at that time or later.

Pl. 6, fig. 8, shows the seed of Colchicum at this time; the embryo and the spongy crest cells are filled with starch.

Pl. 6, fig. 9, shows the cells of Colchicum when nearly ripe; the primary membrane is very distinct, and intercellular spaces occur.

Pl. 6, fig. 10, is a crest cell containing large starch grains.

Fritillaria imperialis and *Convallaria majalis* have no starch in the seeds in the later stages of development, but reserve proteids and oil are associated with the reserve cellulose. In Fritillaria the walls of the endosperm are well thickened, in Convallaria not so greatly. Pl. 2, fig. 8, gives a sketch of the endosperm cells of Convallaria seeds, when the seed is nearly ripe.

Asphodelus luteus, *Anthericum liliago*, and *Tofieldia calyculata* yield no different results from Polygonatum.

Trillium ovatum, in unripe seeds, is very like Paris, starch being associated with a little reserve on the walls. The secondary thickenings are mainly at the corners of the cells, and these swell somewhat in the presence of water; the behavior with iodine is as that of Paris.

SUMMARY.

1. Reserve cellulose appears, as such, on the walls of the cells, soon after the endosperm is formed.

2. Sugar and oil are present in the cells before the appearance of reserve cellulose, and during the process of wall-thickening; of these sugar is first detected.

3. The reserve cellulose appears first at the angles of the cells, and there extends to the walls.

4. The cells of the endosperm, near the chalaza, [illegible] thickened; those next the integuments are next affected; [illegible] are the last to mature.

5. In some seeds (Iris) reserve cellulose in it [illegible] of swelling with water, and going over into a mucila[illegible] [illegible] is noticeable in the mature seed, after long continued boiling in water.

The reserve cellulose of Paris and Trillium seeds swells with water before maturity. This is true of Paris, when the seed is ripe, and will, undoubtedly, prove true of Trillium also.

6. With the exception of Paris and Trillium the association of starch with reserve cellulose has not been observed as a reserve constituent of the cell in seeds of Liliaceae.

In Colchicum, starch is found outside the endosperm in the crest of the ripening seed.

In Galanthus, Scilla, Lloydia, and Narcissus it is found in the endosperm cells during the later stages of the ripening of the seed, perhaps a sign of arrest in processes of development. When the seed is fully matured the starch is not present.

In Convallaria, Fritillaria, Tofieldia, Anthericum, and Asphodelus it is never present in the seed.

In Asparagus and Polygonatum, starch-builders, with minute grains of starch, are found in certain cells of the endosperm before the thickening of the wall begins; during the processes of thickening, they are not visible.

In Iris a little starch appears in the cells of the chalaza, never in the endosperm, before any thickening takes place.

EXPLANATION OF THE PLATES

The drawings are made with [illegible]

PLATE 1.

Fig. 1. Cells from the ripe endosperm of the seed of [illegible] lute alcohol. x 350.

Fig. 2. Cells from the endosperm of *Iris* [illegible]

Fig. 3. Cells from the dry seed of [illegible]

Fig. 4. Cells from the endosperm of [illegible]

Fig. 5. Cells from the endosperm of [illegible]

Fig. 6. Cells from the endosperm of [illegible]

Fig. 7. Cells from the same, in section transverse to the long axis of the cells; from the dry seed, treated with iodine. x 30.

Fig. 8. Cell from the endosperm of *Paris* [illegible] *b*, starch grains; *c*, oil drops. x 350.

Fig. 9. Cells from the endosperm of *Paris* [illegible] with water. The seed is of the same age as [illegible]

Fig. 10. *Lloydia serotina*, cells from the endosperm; from material supposed to be unripe, seeds falling from the capsules; preserved in absolute alcohol; with iodine; starch at *s* nearly covers the nucleus. x 350.

Fig. 11. Cells from the endosperm of seeds of *Lloydia serotina*; material as above; contents of the cells removed with chloral hydrate; at *a*, the floors of the cells show the thin portions. x 350.

PLATE 2

Fig. 1. Section through the endosperm of the seed of *Polygonatum multiflorum*; after boiling 1 min. in H_2SO (1 part H_2SO_4, 5 parts H_2O). The reserve cellulose is dissolved. x 350.

Fig. 2. The same, contents also removed. x 350.

Fig. 3. Section of the seed of *Tulipa gesneriana*, during solution with weak, hot, sulphuric acid; treated with iodine.

Figs. 4 and 5. Sections of *Polygonatum multiflorum* seeds after twenty four days' treatment with cold, weak HCl. x 350.

Fig. 6. Section of Polygonatum seed after eight hours' boiling in water. The section is tangential to the seed; at *a*, the surfaces of the cell walls appear, with the ends of the canals as pits. The canals do not always meet those in the contiguous cells, from the oblique nature of the section. x 350.

Fig. 7. The sketch represents the swollen appearance of the walls of the seeds of *Iris pseudacorus* after eight hours' boiling; *a*, distorted wall; *b*, contents of the cell. x 350.

Fig. 8. Section through the nearly ripe endosperm cells of *Convallaria majalis*. x 350.

PLATE 3.

Fig. 1. Section through the ripe seed of *Polygonatum multiflorum*; A, natural size; B, magnified.

Fig. 2. Section through the embryo of *Polygonatum multiflorum*; before the protruding of the radicle. A, embryo, slightly enlarged; *a*, cotyledon; *b*, hypocotyl; *c*, punctum vegetationis; *d*, nascent vascular tissue; *e*, root-cap, containing starch. B, region about the punctum vegetationis; *d*, cotyledon; *b*, nascent vascular tissue; *c*, punctum vegetationis; *a*, tissue containing starch-formers. x 350. C, cells from the cotyledon, treated with chloral hydrate, and osmic acid; *n*, nucleus; *o*, oil. x 350. D, cells from below the vegetative cone; treated with absolute alcohol, and with iodine; *n*, nucleus; *s*, starch-formers. x 350.

Fig. 3. Section of young plant of *Polygonatum multiflorum* eight weeks after the planting of the seed. A, natural size; B, enlarged. The section has been treated with iodine; *a*, unaltered endosperm, red-brown with iodine; *b*, cells from which the reserve has been dissolved, colorless with iodine; *c*, cotyledon with central vascular shaft well formed; some starch in the cells, and oil in the layer of epithelium cells in contact with the endosperm; *d*, portion of the cotyledon outside the seed, which earlier enclosed the bud; *e*, young bud; *f*, young stem, cells gorged with starch; *g*, root-hairs.

Fig. 4. Younger seedling of *Polygonatum multiflorum* somewhat more enlarged. The cotyledon in this case is curiously lobed; *c*, bud still enclosed in the sheathing cotyledon; *e*, endosperm with undissolved reserve cellulose; *d*, endosperm with reserve cellulose dissolved; *a*, layer of cells rich in oil; *b*, cells containing starch.

Fig. 5. Cells of endosperm from seedling of *Polygonatum multiflorum*, which are in contact with the cotyledon; *e*, cotyledon; *f*, collapsed, exhausted cells; *g*, loose, nearly empty cells. At B, *a*, the cell walls are distorted by pressure from the growing cotyledon. x 350.

Fig. 6. Portion of the endosperm of the seed of *Polygonatum multiflorum*, eleven weeks after planting. The irregular solution of the reserve of the walls is shown; *o*, oil; *n*, nucleus. Small globules of oil, in contact with the wall, are shown. x 350.

Fig. 7. Portion of the seed of *Polygonatum multiflorum* eight weeks after planting. 1. Cells of the cotyledon, containing much oil in the outer row; *n*, nucleus; *s*, inner cells, containing starch formers with starch. 2. Mass of collapsed cells. 3. Cells from which the reserve is dissolved. 4. Cells which show the gradual and quite uniform solution of the reserve; *b*, granular and oily, reserve contents; *o*, oil. x 350.

PLATE 4.

Fig. 1. Young seedling of *Iris pseudacorus* four weeks after sowing the seed. A, *a*, seed with testa; *b*, petiole; *c*, horny tip of petiole, which first appears above the ground; *d*, sheathing portion of the petiole; *e*, stem; *f*, root; *g*, first leaf above the soil. Natural size. B, section of the seed from the same seedling; *a*, cotyledon filled with starch; *b*, endosperm with thickened walls; *c*, endosperm cells, from which the reserve is dissolved. Natural size.

Fig. 2. Section of seedling of *Iris pseudacorus*, still in the soil (with iodine); *a*, endosperm; *b*, cotyledon; *c*, petiole of the same; *d*, horny tip; *e*, sheathing portion; *f*, bud; *g*, hypocotyl. Starch is seen in the sheathing part of the petiole in the bud, and in the hypocotyl. Natural size.

Fig. 3. Section of the seed of *Iris pseudacorus* when the plant was th [illegible] the cells; *b*, vascular portion; *c*, cells from which the reserve [illegible] the [illegible] seed the walls are still thickened; at *d*, the cells are displaced by [illegible]

Fig. 4. Isolated cell from the endosperm, examined in water; *a*, nucleus [illegible] near the walls; the arrows indicate the direction of the streaming of the protoplasm. x 350.

Fig. 5. Seedlings of *Allium cepa* at different stages; *a*, seed; *b*, cotyledon; *c*, root. [illegible] of the food has been absorbed by the coiled tip of the cotyledon. III has [illegible] ground; the cotyledon tip is not green, and is about to wither away. Natural [illegible]

Fig. 6. Section of seed of *Allium cepa* as in fig. 5, II; *a*, cotyledon; *b*, endosperm, with reserve dissolved from the walls; at *c*, the walls are still thickened. Enlarged.

Fig. 7. A few cells from the seed of *Allium cepa* showing the method of [illegible] *b*, spaces between the cells, from which the reserve is dissolved. Not drawn to scale.

Fig. 8. Cells of *Allium cepa* near the edge of the seed; solution of the reserve [illegible]

PLATE 5

Fig. 1. Section of the young seed of *Iris sibirica* in the plane of the long axis; *c*, endosperm [illegible] close-set cells, containing oil drops; *d*, chalaza, with a little starch in the cells; *e*, cells of the outer integument, containing chlorophyll. x 350.

Fig. 2. Endosperm cells of *Iris sibirica* in the unripe seed; the oil has been removed by alcohol [illegible]

Fig. 3. Cells from the close-set layer, in the integument; each contains a greenish yellow oil globule. x 350.

Fig. 4. Cells of endosperm of *Iris sibirica*, at the stage when the thickening of the walls is beginning. The section is in absolute alcohol; *n*, nucleus; *o*, oil.

Fig. 5. Cells from the outer layers of the endosperm of *Iris sibirica*, when only a slight amount of reserve [illegible] present in the seed; *n*, nucleus; *l*, crescent-shaped bodies, which, with the proteids about the nucleus, color red brown with iodine. x 350.

Fig. 6. Cells from the same section as in fig. 4, after water has been applied. x 350.

Fig. 7. Later stage in the swelling of the reserve cellulose in a seed from the [illegible] as in figs. 4 and 6. x 350.

Fig. 8. A few cells from the endosperm of *Iris sibirica* when treated with chloroiodide zinc; *a*, swollen masses of reserve cellulose; *b*, granular matters aggregated by the swelling of certain layers of the cell wall; *c*, protoplasmic membrane still extending to the original wall. x 350.

Fig. 9. Cells from section of *Iris sibirica* seed which was cut transverse to the section in fig. 8. Treatment the same as above. x 350.

Fig. 10. Cells from the close-set layer of the integument, from seeds of *Iris sibirica*, two weeks later than [illegible] x 350.

Fig. 11. Cells from endosperm of *Iris sibirica* after the thickening of the walls had begun. x 350.

PLATE 6

Fig. 1. Early stage of the endosperm cells of the seed of *Polygonatum multiflorum*, before the walls are formed. With absolute alcohol and haematoxylin. x 350.

Fig. 2. Cells of endosperm of *Polygonatum multiflorum*, soon after formation; *n*, nucleus with several nucleoli. x 350.

Fig. 3. Cell of endosperm of *Polygonatum multiflorum*, before the thickening of the wall. The oil has been aggregated by treatment with chloral hydrate; *o*, oil; *n*, nucleus. x 350.

Fig. 4. Cells of the endosperm near the chalaza in a seed of *Polygonatum multiflorum*, before any reserve cellulose has appeared in the endosperm; *n*, nucleus, with starch-grains in the starch-formers, in the neighborhood; with absolute alcohol and iodine. x 350.

Fig. 5. Cells from the seed of *Polygonatum multiflorum*, when the reserve cellulose first appears in the cell; *n*, nucleus; *a*, reserve cellulose. x 350.

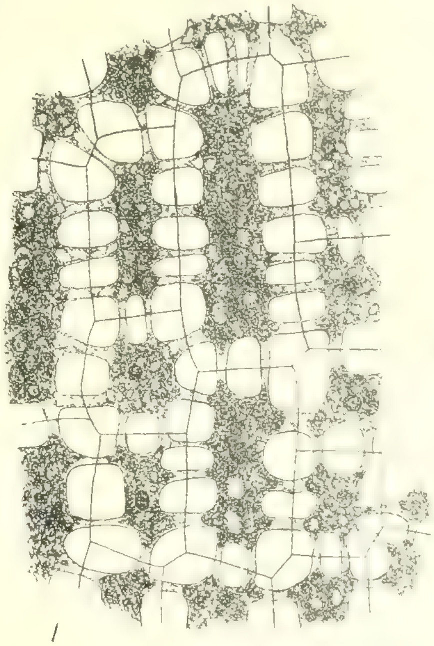
Fig. 6. Cells from the same endosperm as in fig. 5, where the thickening has proceeded farther. The two sketches are from sections treated with iodine; *n*, nucleus. x 350.

Fig. 7. Cells from near the center of the endosperm of *Galanthus nivalis*, in the later stages of ripening. Only a few cells remain with unthickened walls; with iodine; *n*, nucleus; *s*, starch. At B the surface of some of the cell walls is shown with points of less thickening at *a*. x 350.

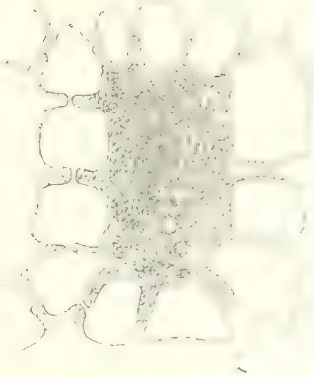
Fig. 8. Section of nearly ripe seed of *Colchicum autumnale*; *a*, embryo, containing starch; *e*, endosperm; *c*, crest of the seed containing much starch. Enlarged.

Fig. 9. Endosperm cells of *Colchicum autumnale* when the seed is nearly ripe; with iodine; small intercellular spaces occur at the corners. x 350.

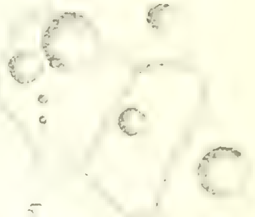
Fig. 10. Cell from the crest of the seed of *Colchicum autumnale*, when nearly ripe; large starch grains are present. The section was treated with iodine. x 350.



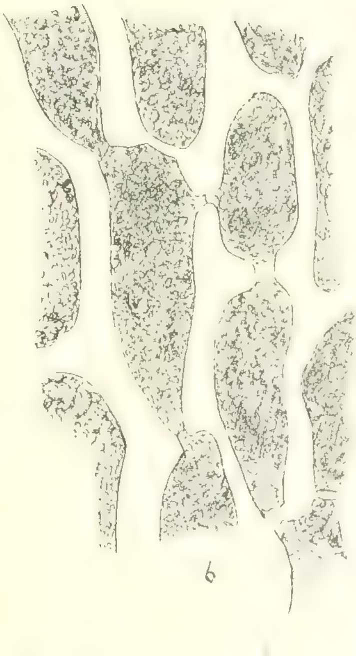
1



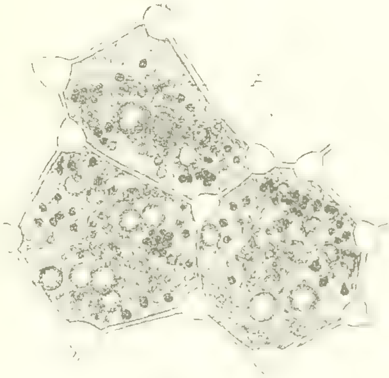
4

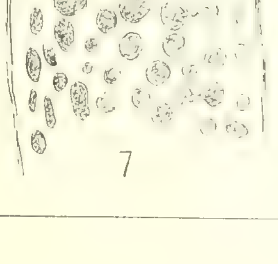


5

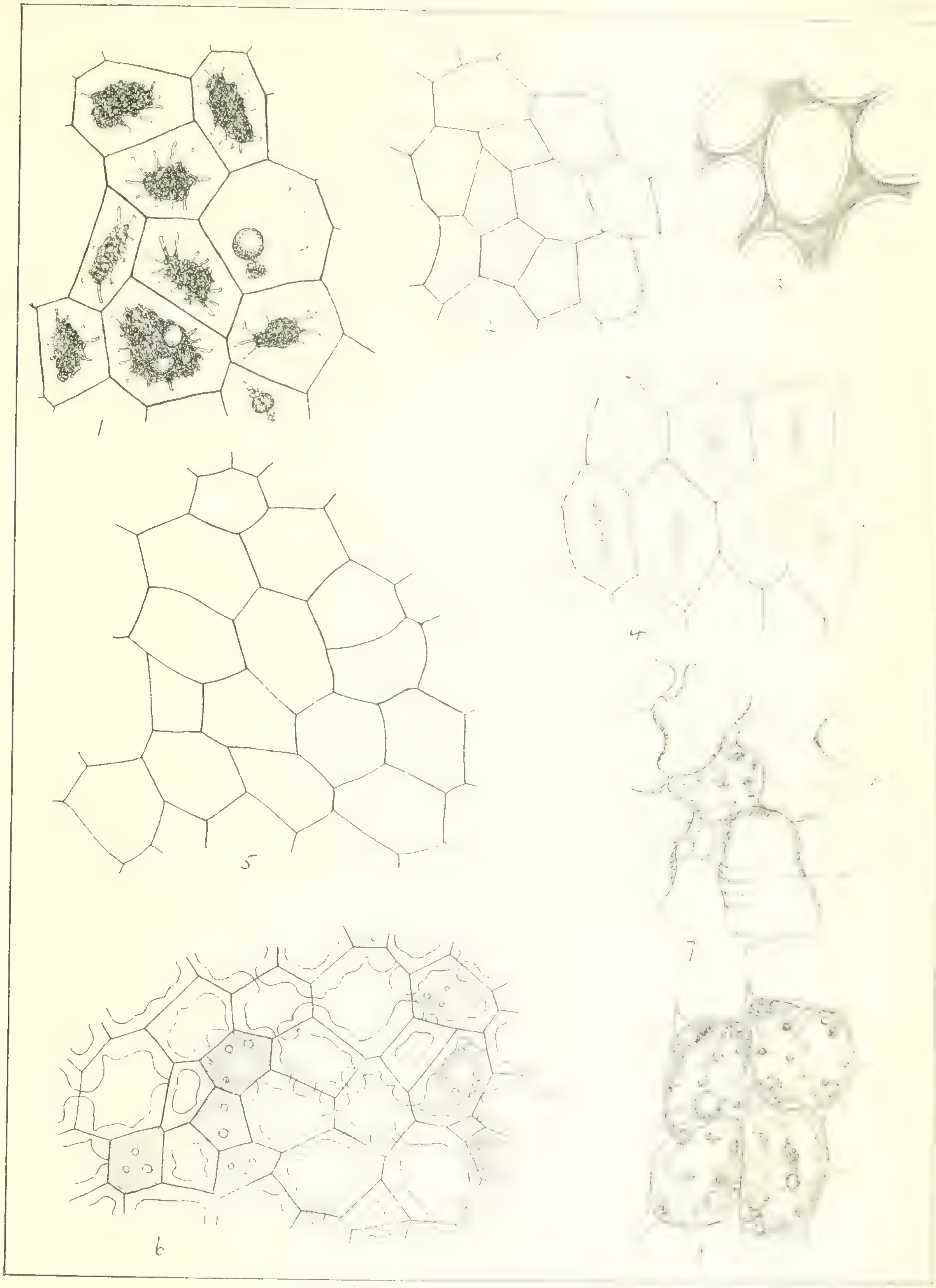


6

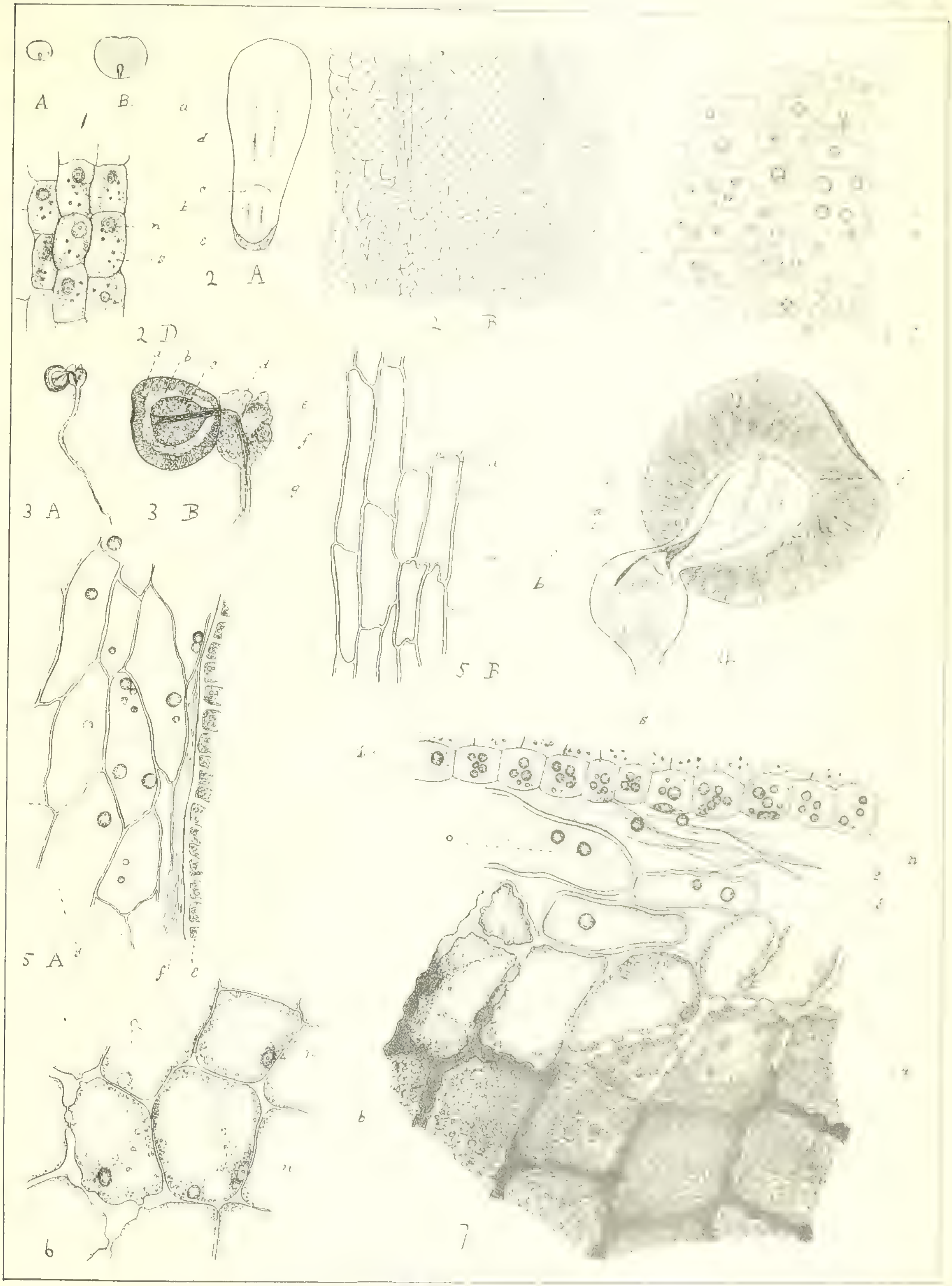


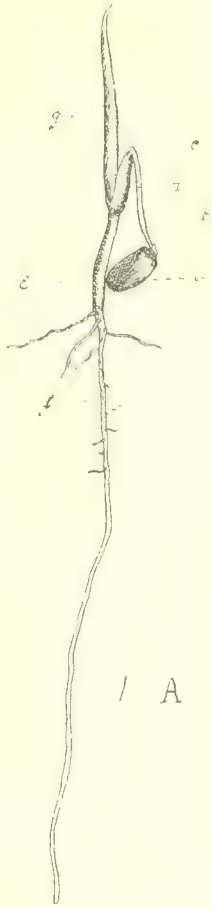


7



COOLEY. RESERVE CELLULOSE.


A
B.
1
n
s
a
d
c
b
e
2 A
2 B
2 D
a
b
c
d
e
f
g
3 A
3 B
a
b
4
5 A
f
e
5 B
6
n
7
s
n
b



1 A

1 B

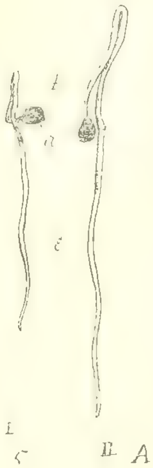
2

3

4

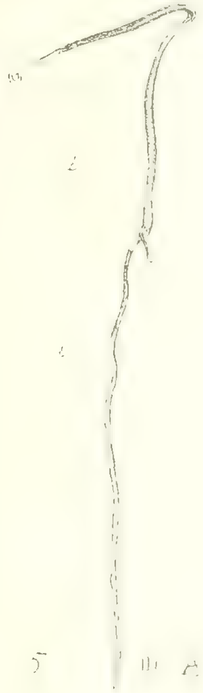
6

7

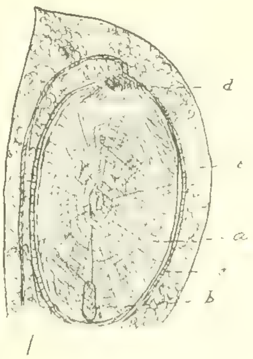


I
5 II A

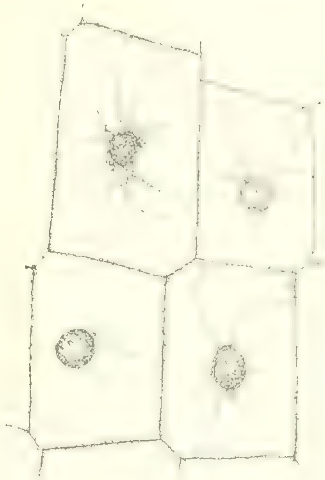
5 F



5 III A

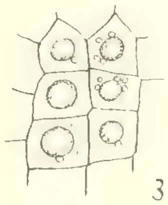


1

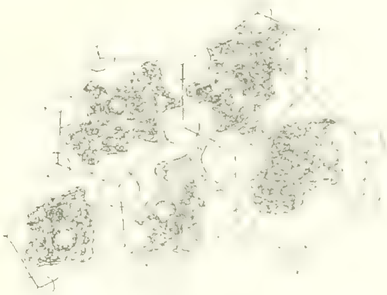


2

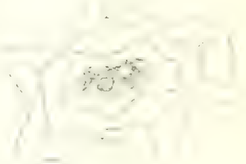
4



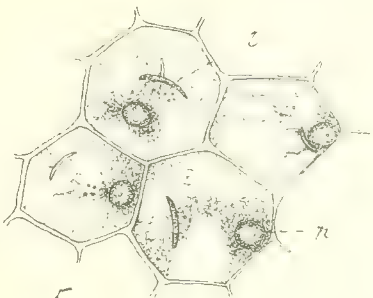
3



6

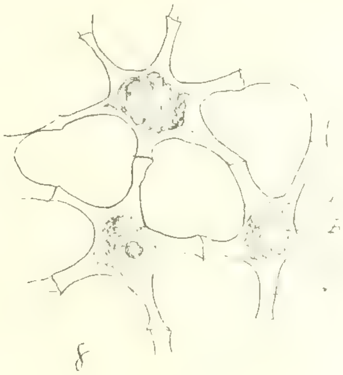


7

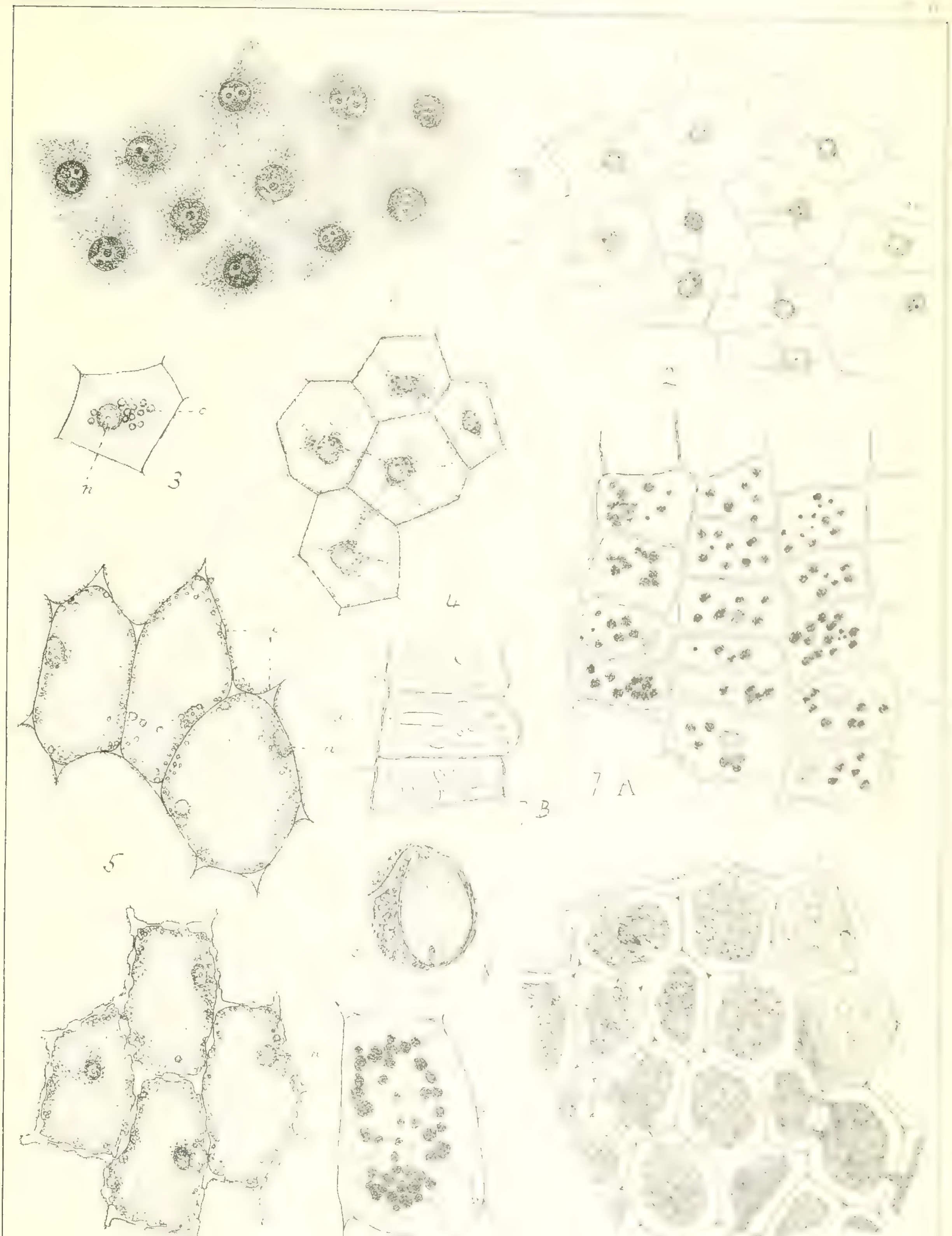


5

9



8


2
c
n
3
4
c
n
5
B
7 A
n
6

NOTES ON THE DISSECTION AND BRAIN OF THE [illegible]

(*Troglodytes niger*)

BY THOMAS DWIGHT.

Read [illegible]

"Gumbo" was a very fine male chimpanzee who at one time was [illegible] zoological gardens at Lisbon. He was leased to a museum at Boston [illegible] the autumn of 1894 of general tuberculosis. He had probably [illegible] full size, though the last of his second teeth had not taken their [illegible] some of the epiphyses were distinct. Before his sickness he was remarkably muscular. He is said to have been very intelligent, but was not trained to rival "Sally." His temper was violent. I regret that I never saw him alive. Even after death he did not come into my hands until after the autopsy. This was performed more than twenty-four hours after death. The progress of putrefaction combined with the effects of tuberculosis had made the condition of the thoracic and abdominal cavities truly frightful. The viscera and skin were practically worthless. The brain, happily, was perfectly healthy. The body was then sent to the Harvard medical school and dismembered as soon as possible. There was a great deal of very black hair about the face. Indeed, the hair was black, or nearly so, everywhere. There were bare spots, almost callosities, over the tuberosities of the ischia.

The height, measured after the removal of the brain, from vertex to heel, the leg being straightened as much as possible, was about 131 cm. This must be regarded as only approximate.

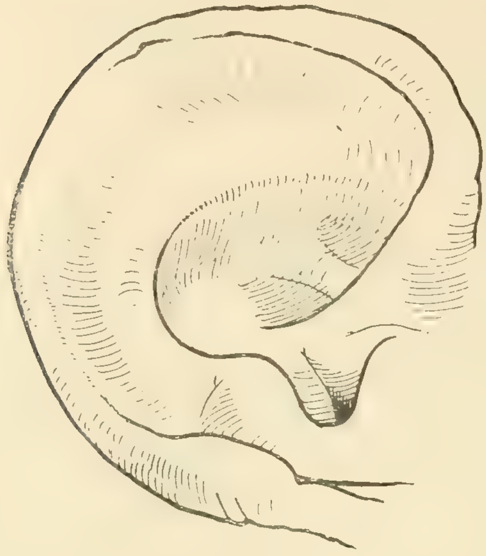
The length of the hand from the fold at the wrist to the end of the middle finger was 24.4 cm. on the right. The left was 1 mm. longer. The length of the foot to the end of the third toe was 24.7 cm. on the right, and 2 mm. less on the left. The great toe resembled strikingly a human thumb, and the lines on the sole of the foot were much more like those of the human hand than were those of "Sally" as shown in Mr. Beddard's[1] figures. The lines of the hands and feet are well shown in the reproductions of the photographs (pl. 7).

The ear is admittedly very variable in the chimpanzee. Those of "Gumbo," like those of the *T. aubryi*[2] and of "Mr. Crowley," the New York [illegible] human than those of "Sally" which are prolonged further upwards away from the head. In "Gumbo" the two are very unlike. Their proportions differ considerably. The right one is 8 cm. long by 6 cm. broad, while the length of the left is 8.7 cm. and its breadth 5 cm. The length in the *T. aubryi* is 7 cm., that of "Mr. Crowley's," taken from a cast, is 9 cm. and the breadth 5.5 cm., that of "Sally," taken from the life-size illustration, is length, 7.6, breadth, 5.3 cm.

---

[1] Trans. Zool. Soc. London, vol. 13, 189[illegible]

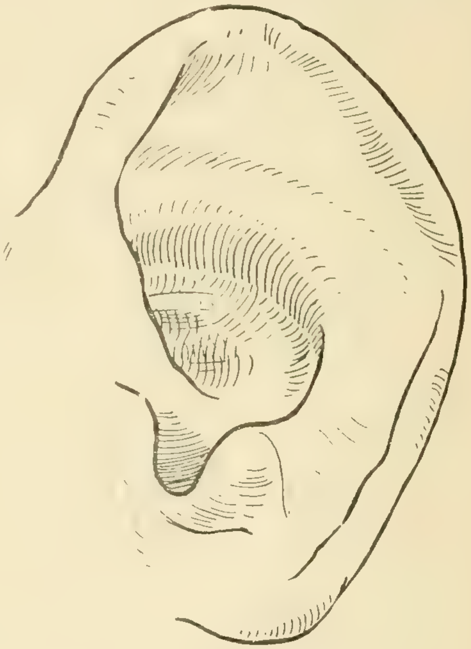
[2] [illegible]



Right Ear.

In "Gumbo" the notch is well marked on both sides, but narrower in the narrow left ear. There is a very rudimentary lobule, stronger on the left. This is present in the *T. aubryi*, and quite wanting in "Sally." The ascending part of the helix of the left ear folds over much more strongly than on the right, but the fold is interrupted at the top on the left, while in the right it is continued into the posterior border. After this interruption, however, the fold of the helix along the back of the ear is stronger on the left than on the right.

It would be presumptuous to dispute with the distinguished authorities who declare that there is more than one species of chimpanzee. There can be no question, however, that the range of individual variation is very great in the details of the skeleton, of the muscles, and of the brain. It has not seemed advisable to publish a full description even of those parts of this animal which could be thoroughly studied. In this paper particular attention is given to the brain and to peculiarities in the muscular system of the extremities.



Left Ear.

THE AGE.

According to very vague information which I have received, this animal was ten or twelve years old. "Sally," who lived more than eight years at the zoological gardens in London, was thought to be about two years old when she came. The chief criterion of age being the teeth and the progress of ossification, it may [illegible] at this point and to compare them with "Sally's."

TEETH.

The second dentition was complete, excepting that [illegible] not very much more than cut the gum. The fangs of the third [illegible] had not yet reached their full development. The left inter[illegible] and the two left inferior incisors are wanting and no signs of their alveoli remain. There is reason to fear that they had been drawn in order to teach the animal to smoke. The teeth of the upper jaw in this neighborhood are much distorted, the canine projecting forward and outward, and the lateral incisor being bent strongly inward. The first premolar of that side has practically no roots. The bone is hypertrophied internal to the displaced socket of the canine. The crowns of the molars are little worn. In the upper jaw they are of very nearly the same size, but in the lower jaw the crown of the second is the largest and that of the first rather the smallest. In the upper jaw the first and second molars have two external and two internal cusps, the third differing in having only one internal one. In all of them the internal cusps are not at the edge of the crown, but separated from it by a considerable oblique surface. I fail to recognize any distinct oblique ridges between the cusps. Each of the inferior molars has three distinct external cusps. The first and second have two internal ones. The posterior of these latter is indistinct on the right third molar and wanting on the left one. Barring this, the inferior molars resemble those of the *T. aubryi*.

Mr. Beddard gives the following account of "Sally's" dentition: "In the upper jaw the permanent incisors and bicuspids are present; the first molar is the only one of the molar series which is in place. The canines are a long way from their definitive position; the point of the tooth is fully half an inch from the rim of the socket; the extremity of the root of the tooth is barely half an inch from the rim of the orbit. . . . The milk canines are the only representatives of the milk teeth which have not been replaced." It is clear that "Gumbo" is further advanced. I do not presume to say what period of time this difference represents. It goes to show, however, that he can hardly have been younger than ten and may well have been a year or two older. This is important as showing the progress of ossification at that age.

OSSIFICATION.

The cranial sutures are distinct, but none of the bones show any disposition to fall apart after maceration; indeed, they could not be separated without injury. The suture between the basi-occipital and the basi-sphenoid is quite open on the outside of the base, and closing within. (I have observed that these surfaces in the human skull join in the same order.) All traces of sutures between the maxillae and premaxillae are lost.

The upper epiphysis of the humerus and the lower one of the femur are still separate; those at the other end of these bones have joined. The radius and ulna have the lower epiphyses free and the upper ones fused. In the tibia the lower end is still free and the upper has but very recently united by bone. In the fibula both ends are still free. The scapula has the end of the acromion and the inferior angle free; the posterior border is still rough, but if any distinct epiphysis existed it has been lost. In the innominate bone there is a very faint trace of suture remaining opposite the acetabulum. The epiphysis over the tuberosity is joined, but its continuation on to the ramus is presumably lost. The crest is unfinished. The plates on the bodies of the vertebrae are in many instances (probably in most) still separable. In the sternum the manubrium is, of course, distinct. Cartilage still separates the first piece of the mesosternum from the others which form one bone. The ensiform is wholly cartilaginous.

THE SKELETON.

The skull. This, like the rest of the bones, is large and strongly marked. Greatest length from posterior occipital protuberance to the front of the premaxillae, 19.5 cm. Greatest breadth a little back of ear in the continuation of the occipital curved line, 13.1 cm. Cranial capacity 430 cc. The temporal ridges are strong. Their nearest approach to each other is 5 cm. in the frontal region; their greatest separation is 9.5 cm. at their termination. The orbital borders are rather more strongly raised than in most skulls. The interorbital region is concave vertically. The orbital index of the right orbit is 100; that of the left, 88. (The transverse diameter is taken to the posterior border of the lachrymal groove.) Observations on several chimpanzee skulls impugn the statement that the transverse diameter of the orbit always considerably exceeds the height. The sphenoidal fissure is small; seen from the inside it does not appear much larger than the optic foramen. Beddard mentions its large size in *T. calvus.* Sutton[1] states it is large in *T. niger.* The extremity of the petrous is nearly 1 cm. in advance of the suture between the basi-occipital and sphenoid on the outside of the skull; on the inside the distance between them is more than half as great. The crista galli is rudimentary. The fossa above the cribriform plate is very deep; much deeper than in "Sally," as is shown by the brain.

---

[1] Journ. anat. physiol., vol. 18.

The spine. The vertebral formula is C. 7 T. 14 L. 3 S. 6 C. [illegible] the coccyx is narrow and elongated. It may represent [illegible]. The head of the first rib encroaches on the seventh cervical vertebra. The head of the fourteenth, about 10 cm. long, rests on a little elevation on the vertebra. Almost touching the head is a rudimentary tubercle. The cartilages of seven ribs reach the sternum.

The greatest length of the humerus is 31.7 cm., and that of the femur, 32.3 cm. This is stated by way of giving an idea of the size of the bones, which is important in connection with the process of ossification.

There are few points in the bones of particular interest. As usual, there is no supra-trochlear perforation of the humerus. Each femur has a small, but well-marked, third trochanter, and below it a shallow, roughened groove, the fossa hypo-trochanterica (pl. 8).

MUSCULAR SYSTEM.

The muscular dissection was limited to the extremities. The plan which I pursued (with some few lapses) was to describe what I found without refreshing my memory as to chimpanzee anatomy. When this was done, I consulted the authorities. I have made especial use of Mr. Hepburn's[1] account of the limb-muscles of the four anthropoids. I give only what seems to me interesting or peculiar. The most important points are probably the arrangement of the flexors of the fingers, the anomaly of the pronator quadratus, the redundance of interossei in both hand and foot, and perhaps the peculiarity of the femoral adductors.

UPPER EXTREMITY.

Latissimus-dorsi and *dorso-epitrochlearis.* The latissimus joins the edge of the teres major and receives fibers from it, which might be said to represent a scapular head. The epitrochlear muscle springs from the anterior aspect of the tendon of the latissimus; is perhaps 1 inch broad at origin, runs to tip of the internal condyle, the last 2 1-2 inches being tendinous. This resembles strikingly Beddard's account of "Sally" and differs from all Hepburn's anthropoids.

Deltoid. Strong. The clavicular part closely connected with the greater pectoral which would appear to be the rule. Some of its fibers seem to join the brachialis anticus.

[1] [illegible]

Coraco-brachialis arises from the coracoid and from the internal border of the short head of the biceps for some 4 inches. It is pierced by the musculo-cutaneous nerve. It divides into two parts. One, tendinous, is inserted into the inner part of the front of the humerus from a little above the middle to the junction of the second and lower thirds or even further. The other part, chiefly muscular, is inserted into the internal muscular septum in the lower third of the arm and by an expansion into the fascia of the arm, being fused with the termination of the dorso-epitrochlearis.

Triceps. The only point to be noted is that, besides its usual insertion, it expands into the fascia of the back of the fore-arm.

Pronator radii teres has two heads with the human relations to nerve and artery (*vide flexor carpi radialis*).

Palmaris longus is inserted more to the radial side than in man.

Flexor carpi radialis. Besides the usual origin it arises from the oblique line of the radius by a fibrous layer which gives origin to the fibers of the pronator teres ; below the oblique line it arises from the anterior border of the radius to within two inches of the lower end. It is inserted into the base of the second metacarpal. This origin resembles that seen in the gorilla but not in "Sally" nor in Hepburn's chimpanzee. The insertion is the same as that seen in "Sally." In both respects it agrees with Gratiolet and Alix's *Troglodytes aubryi.*

Flexor carpi ulnaris. A tendinous slip arises high up from the deep aspect of its ulnar aponeurosis of origin. From this a series of short muscular fibers run obliquely downward and outward to another parallel tendon which, lying superficial to the flexor tendons of the fingers, is inserted into the annular ligament to the radial side of the pisiform, which bone receives the main tendon. The ulnar nerve comes to the surface between the two tendons. (The deep tendon gives origin to some fibers of the flexor sublimis digitorum.)

This may be called either a double insertion of this muscle, or we may say that there is an extra palmaris longus. Something resembling this seems to have been seen in gorilla by Duvernoy.

Flexor sublimis digitorum arises (1) from the common condyloid muscular mass and septa within it, (2) from the coronoid, and (3) from the oblique line of the radius. This head is attached also along the anterior border to within about 2 1-2 inches of the lower end. The tendon of the little finger arises from the superficial mass on the ulnar side. The tendon of the annularis arises from the superficial mass more anteriorly. It receives an insignificant reinforcement from the top of the oblique line of the radius. The tendon of the middle finger receives its fibers from the coronoid head and from practically the whole radial origin, whence the fibers run into the edge and anterior surface of the tendon. This is much the largest tendon. That of the index arises as a small muscular belly from the coronoid, soon becomes tendinous, and sends a small muscular bundle to the division for the third finger. It then gives off a series of short oblique fibers, which run to another parallel tendon which is the terminal one. It passes obliquely under the others just above the wrist. The three inner tendons pass under the annular ligament in the same plane, that for the little finger being a shade behind.

Expressed differently, the condyloid head supplies the fourth and fifth fingers (the latter receiving a trifling bundle from the radius). The coronoid head goes to the middle finger and index. The radial head goes to the middle finger.

N. B. A connecting link with the flexor profundus arises as a muscle, perhaps 1-2 inch broad and from 5 to 6 inches long, from the coronoid portion. Its tendon becomes the deep tendon of the index and receives on its radial side the fibers of the radial portion of the muscle next described.

Flexor profundus digitorum is very clearly divided into a smaller radial and a larger ulnar part. The former arises from the front of the radius and a little of the interosseous membrane; all its fibers go into the connecting link just described, which is the tendon of the index. The ulnar portion (separated from the radial by the anterior interosseous vessels and nerves) divides into three tendons. That for the minimus comes from a muscular belly that is distinct nearly half way up the fore-arm. The other two are much more closely connected. The ulnar portion also gives some muscular fibers to the index tendon.

Flexor longus pollicis has *no* existence whatever as a muscle. A minute tendon first appears a little above the annular ligament as a thickening of the delicate sheath of the radial part of the *flexor profundus*. As it descends it grows stronger, becoming a well-defined little tendon, perhaps 1.5 mm. broad, going to the second phalanx of the thumb. This has been repeatedly seen in the chimpanzee, but usually the tendon comes directly from the muscle.

There can be, I think, no question that in this flexor group the anthropoids exhibit much individual variation. The accurate comparison of the different descriptions is more wearisome than profitable, owing to the complication of the structure. The accounts all differ more or less. The connecting slip from the superficial flexor to the deep one is not normal in the chimpanzee, but occurs as an anomaly as it does in man. In "Sally" such a slip was found going to the deep tendon of the ring finger.

Lumbricales are four in number. The first arises from the radial side of the tendon of the index; the second from the other side of this tendon and the radial side of the tendon of the medius. The third springs from the neighboring sides of the tendons of the medius and annularis; the fourth from the ulnar side of the latter. The accounts of these muscles in various chimpanzees show trifling differences in most cases.

Pronator quadratus. Similar on both sides. It is in two layers which are only partly separable. The more superficial begins as a tendon at the top of the ulnar origin and expands as it passes downward and outward across the muscle. It gradually becomes muscular, and having reached the outside of the radius, runs downward (hidden by the flexor carpi radialis) to the ridge of the trapezium. It is about 7 mm. broad at the end. The deeper, more transverse part of the muscle runs somewhat slanting downward to the radius. A few fibers near the radial side go to the front of the capsule of the wrist.

This is an anomaly very rarely observed in man. I cannot find any record of it in the chimpanzee. Macalister observed it in a Bengal tiger, though it is not normal in the Felidae. It seems to show that animals of diverse groups have a tendency to similar variations which are not determined by heredity.[1] I am not aware that the pronator quadratus as above described is normal in any mammal.

Palmar muscles of the thumb. Abductor brevis runs from the annular ligament and sesamoid bone to the base of the first phalanx. Its tendon, reinforced by the flexor brevis, passes into an expansion with a tendinous insertion into the second phalanx.

Opponens pollicis from the annular ligament more or less fused with the flexor brevis.

Adductor pollicis transversus from the fibrous aponeurosis which is stretched over the fourth metacarpal. It arises directly from the distal part of the third metacarpal. There is a slight interspace allowing it to be divided into a proximal and a distal part; both in the same plane.

Adductor obliquus from the base of the third metacarpal to the usual insertion and by a very small tendon to the second phalanx.

Flexor brevis has no inner head. Hepburn found a rudimentary one.

Palmar muscles of the little finger. Practically as in man.

The *interossei* are discussed after the other muscles of the fore-arm.

Extensor communis. Not remarkable. Portion for index easily separable in the lower third of the arm. The tendon for the little finger sends fibers to the fourth. Wilder[2] found no tendon to the little finger.

Extensor minimi digiti. This supplies both the fourth and fifth fingers (as Hepburn describes for the orang-outang and Beddard for "Sally").

The action of the extensor tendons seems to be nearly limited to the first phalanges.

---

[1] The significance of anomalies. Amer. nat., Feb., 1895.

[2] Proc. Bost. soc. nat. hist., 1861.

Abductor pollicis longus to trapezium and sesamoid bone.

Extensor primi internodii pollicis is so fused with [illegible] one muscle with two tendons; it is inserted into the base of the [illegible] on the radial side (better called extensor pollicis brevis).

Extensor secundi internodii pollicis, vel extensor pollicis longus, arises from the lower part of the ulna and interosseous membrane into a fibrous expansion [illegible] the back of the thumb, and is inserted into the second phalanx.

Extensor proprius indicis is a small muscle going to the index only; in Hepburn's chimpanzee it sent a slip to the ring finger.

Interossei manus. There are four dorsal, practically the same as in man. There are seven palmar; namely, two for the index, the middle and ring fingers, respectively, and one for the little finger. The smallest of these is the first. It arises from the radial side of the metacarpal bone of the index internal to the belly of the dorsal. The second is a large one on the ulnar side of the index. The third and fourth lie on the metacarpal of the middle finger, touching each other and arising in part from a fibrous septum between them. The third receives also a few fibers from the base of the second metacarpal. The fifth and sixth arise (excepting for the last detail) in a similar manner from the fourth metacarpal. The seventh arises from the radial side of the fifth metacarpal and from the hook of the unciform.

There is (with one exception) an important difference between the insertion of the dorsal and palmar interossei. The dorsal are attached to the sides of the bases of the first phalanges, still the chief action is to flex them; lateral movement is not great. The palmar ones end in well-defined tendons which run along the sides of the first phalanges and end in the fibrous expansion over their dorsal aspects. Their chief action is to flex the first phalanges and extend the second and third. The exception alluded to is the first palmar which has a very small tendon more or less fused with that of the first dorsal.

The chimpanzee has been described as having six palmar interossei, my little first one not having, I believe, been hitherto observed. I have called it a palmar interosseous because it seems to me a distinct muscle; still its mode of termination gives support to those who would call it a part of the first dorsal. For the others not found in man I cannot admit this interpretation. They are all in the same plane and have a similar insertion. Compare Hepburn on anthropoids, Cunningham on Thylacine (Journ. anat. physiol., vol. 12), and Champneys on chimpanzee (ibid., vol. 6).

LOWER EXTREMITY.

Gluteus maximus. Origin as usually described, including a thick portion from the tuberosity of the ischium. It is inserted into the fascia lata, into the gluteal ridge and back of the femur quite down to the external condyle and joining the tendon of the biceps at the knee. This is a somewhat lower insertion than is usually described.

No separate *tensor vaginae femoris.* A small one is usually found.

Scansorius arises from the anterior border of the ilium and is inserted in common with the gluteus minimus.

Pyriformis inseparably connected with gluteus medius.

Gemellus superior, broad; *gemellus inferior*, small.

Quadratus femoris. A small muscle, arising from the front of the tuberosity of the ischium, runs to the posterior intertrochanteric line, reaching lesser trochanter. (I do not find Hepburn's vertical part.)

Biceps femoris. Has the two parts distinct. The ischial portion goes to the head of the fibula, sends an expansion to the front of the external tuberosity of the tibia, and is connected with the sural fascia. The femoral portion runs to the head of the fibula and to the fascia of the calf.

Quadriceps extensor, differing from that of "Sally," is easily separable into four parts. The *vastus internus* overlaps the cruraeus from which it is much more distinct than is the vastus externus. *Rectus* has both heads.

Gracilis seems three or four times as strong as *sartorius;* they both end in broad expansions which are inserted more than one third and one half way down the leg, respectively.

Adductor group is very puzzling.

Pectineus is small, but distinct.

Adductor magnus arises from the tuberosity of the ischium and runs down as a thick round belly to the adductor tubercle. This seems to be the whole muscle, being perfectly distinct. The femoral artery passes back between it and the muscle now to be mentioned, to become the popliteal. This is an extremely thick and strong muscular mass arising from the front of the pubes and from the pubic arch and running to the linea aspera. Separate muscles are not to be made out. I recognized no *adductor longus* nor *brevis.* It represents all the adductors of human anatomy except the vertical portion of the adductor magnus. This division of the adductor magnus into two parts is normal in the chimpanzee, but the fusion of one part with the other adductors is peculiar. Wilder found [illegible] adductors present but more intimately connected than in man.

The anterior muscles of the leg, the *peronei*, those of the calf, present nothing noteworthy. The *plantaris* is present and distinct, going partly to the *tendo Achillis* and partly to the fascia at the inner side of the ankle. This muscle seems to be [illegible] often wanting as present. An insertion much like the present one is described by Humphry.

Peroneus longus and *brevis* are inserted respectively to the base of the first and of the fifth metatarsals. Neither has any further insertion.

Extensor brevis is remarkable only for the fact that the first division sends an additional insertion to the second phalanx of the great toe.

The tibial and fibular flexors (*flexor longus* and *flexor hallucis*) are inserted as follows: the former goes to the second, fourth, and fifth toes, the latter to the first, third, and fourth.

Flexor brevis is very small, arising in part from the os calcis. It divides into three little tendons for the second, third, and fourth toes. It receives muscular fibers in common with the lumbricales from the tendons of the long flexors which go to the third and fourth toes. This muscular slip represents the *flexor accessorius*.

Lumbricales are four in number. The first arises from the tendon of the tibial flexor, the others from the tendons of the fibular flexor.

The head of *flexor brevis* from the tendons is very confusingly mingled with the *lumbricales*.

Adductor hallucis transversus arises from nearly the whole length of the fourth metatarsal and from the distal ends of the shafts of the second and third.

Adductor obliquus is hardly separable from the preceding. It arises from the sheath of the *peroneus longus* at the basis of the second and third metatarsals.

Interossei pedis. There is a great complication of these muscles, there being five or six both dorsal and plantar. The reason for this vague enumeration appears in the description.

Dorsals. First muscle from the first and second metatarsal bones to the tibial side of the second toe. The second and third muscles arise each from two bones, and are inserted into the two sides of the medius, thus placing the base line in this toe. The fourth muscle is a very small one, placed on the dorsal aspect of the fourth metatarsal and inserted on the tibial side of the phalanx. The fifth and sixth muscles arise together from the last two metatarsals and are inserted into the adjacent sides of the last two toes. This might be called a single muscle with two insertions.

Plantar interossei. The first is where it should be, on the fibular side of the second toe. The second and third are extra muscles, each arising from one side of the third metatarsal and inserted into either side of the phalanx. The fourth passes from the tibial side of the fourth metatarsal to its phalanx. The fifth arises from the fibular side of the fourth metatarsal and is attached to both the fourth and fifth toes as is the dorsal. It differs from it by arising only from the fourth metatarsal. This excessive redundancy of interosseous muscles in the foot has not, I believe, been observed.

HEART.

The heart and great vessels, removed with the lungs, were in the center of a mass of disease intensely repulsive. At my request a veteran dissector undertook to make a careful dissection of the roots of the lungs and the chief vessels. He was obliged after several hours' work to give up the task. The heart was therefore cut off from the rest. The left auricle was cut so close that nothing of the pulmonary veins is to be seen. The branches of the aorta could not be followed. Their identification is, however, from the manner of their arrangement, practically certain.

The length of the heart (after preservation in alcohol) is 11.5 cm. and its breadth about 8 cm. The external appearance is not unlike that of the human heart. It seems relatively broader, and the origin of the aorta is less concealed by the pulmonary artery. The *conus arteriosus* is well marked; so are also the auricular appendices. The arch of the aorta gives off first an innominate artery about 1 cm. long which divides into the right subclavian and the right carotid. After an interval of 2 mm. the left carotid and the left subclavian arise close together, so close as at first to suggest a second innominate. A minute vessel springs from the aorta just in front of the interspace between the innominate and the left carotid, very probably a *thyroidea ima*, since Sutton has seen this. The subclavian arteries are much larger than the carotids, the lumen of the right subclavian being nearly 6 mm. in diameter and that of the right carotid less than 4 mm. Both these vessels on the right side are a little larger than their fellows of the left. Gratiolet and Alix, while noting this discrepancy between subclavians and carotids in the *T. aubryi*, comment on the relatively small size of all the four great arteries. In this subject the carotids seem to me relatively as large as in man, and the subclavians relatively larger. The diameter of the lumen of the aorta immediately after the origin of the left subclavian is about 1 cm.

Dr. Arthur Keith[1] finds accounts of the origin of the great vessels in eleven chimpanzees. In seven the plan was as in man. In three the left carotid sprang from the innominate. This, it may be noted, is not an uncommon arrangement in man. In one case, that of Chapman, there was a short left innominate for the left carotid and subclavian. Dr. Keith remarks: "Such an origin for the left carotid will probably be found to occur as a prevailing variation in the chimpanzee, for in another individual of that genus an approximation to that condition was observed." The last words express precisely the case of "Gumbo."

---

[1] Journ. anat. physiol., vol. 29.

Inside of heart. The right auricle much as in man. There is a well-marked *annulus ovalis.* The *fenestra* is completely closed. There is no remnant of an Eustachian valve, but on the right wall there is a long, slightly raised valvular fold separating the smooth part of the cavity from that part of the anterior wall bearing the *musculi pectinati.* The fold starts from the right side of the opening of the coronary sinus and runs upward and forward on the outer wall with an anterior concavity. The greatest height to which the valve could be raised from the wall could hardly exceed 3 mm. Its function, at most a very slight one, must be to hinder the regurgitation of blood towards the *atrium.*

The left auricle shows a lunated depression on the septum. The walls are smooth except in the appendix which is smaller than the right one.

The walls of the right and left ventricles present about the relative thickness observed in man. The cavity of the right ventricle is traversed about half way up by a muscular moderator band some 3 mm. in diameter. The three parts of the tricuspid valve are not very easily distinguished. There is a large right one and a large septal one which meet behind. A small infundibular segment might be reckoned a part of the right one. The inside of the right ventricle presents a great development of *columnae carneae.* The interior of the left ventricle is striking. The surface of the septum is perfectly smooth except near the apex. The outer side presents a wonderful network. The mitral valve is as in man.

The great arteries were not split open, so that the valves cannot be thoroughly examined. They apparently are not remarkable.

THE ARTERIES.

The axillary artery gives off an anterior and a posterior circumflex which arise from a common trunk. The posterior runs round the neck of the humerus as in man, with the circumflex nerve. It sends a branch down the back of the arm between the external and the long heads of the triceps.

The brachial artery runs as in man. It gives off almost at its origin a branch which supplies the inside of the arm and another which runs with the musculo-spiral nerve. The two presumably represent the superior profunda. Later a small branch runs to the under side of the biceps, and a few supply the elbow joint. The division into radial and ulnar occurs about one inch below the elbow joint. The whole arrangement is as in man (very different from *T. aubryi*) ; the radial descends in the usual way to the *tabatière*, and then passes into the depth of the palm. The ulnar, which is the larger branch, passes under the pronator teres, the deep head of which separates it from the median nerve. Its distribution in the hand is essentially human. An interosseous artery was given off which was subsequently lost.

With the exception above mentioned this in essentials corresponds to other chimpanzees.

The femoral artery about one inch below Poupart's ligament gives off a small external branch, probably the external circumflexa ilii, and, a little lower, a small one running internally. At about the same level the profunda arises from its deep aspect. From this springs an external circumflex which divides into ascending and descending branches and a small lateral one. The descending runs on the vastus externus to the outside of the knee. The profunda runs probably[1] through the thick mass of adductor muscles, sending back perforating branches.

The femoral runs anteriorly to the adductor mass to the inside of the lower third of the thigh, where beneath the sartorius and the anterior border of the gracilis it divides into the popliteal and the saphenous. The popliteal, which is rather the larger of the two, passes back external to the muscle representing the vertical part of the adductor magnus. Besides articular branches it gives one long sural branch and divides into the anterior and posterior tibials. The former passes forward at once as in man and descending to the ankle ends in a network over the metatarsal bones. The posterior tibial gives off a peroneal branch, neither of which was fully traced.

The saphenous artery gives a considerable branch to the inner side of the knee joint and passing between the *sartorius* and *gracilis* comes to the surface opposite the inner tuberosity of the tibia. It then runs down along the inner side of the leg in company with a vein *beneath* the fascia. It crosses above the internal malleolus to the front of the foot and plunges into the sole between the bases of the first and second metatarsal bones.

Gratiolet and Alix describe the arteries of the lower leg practically as here. They say, however, of the saphenous artery that "Elle se place superficiellement sous la peau, le long de la face interne du tibia, etc.," while I find it beneath the fascia. Zuckerkandl[2] does not touch on this point. My observations, though less minute, agree with his, only that he finds the peroneal springing from the anterior *tibial*.

---

[1] I regret that my notes on this point are not perfectly clear.

[2] Anat. hefte, 15, 1895.

The Larynx.

The general shape and structure are well known. Seen from above and behind (the posterior wall of the cricoid having been divided in the median line), the larynx is proportionately narrower than in man. The epiglottis is smaller and far less prominent. The fossae at the back of the tongue and the glosso-epiglottidean folds are much less marked. Another and more important consequence is, that the aryteno-epiglottidean folds bounding the entrance to the larynx proper do not project nearly so freely as in man. The notch behind is narrower and deeper. The prominence on either side formed by the cartilage of Santorini is further forward, taking the place occupied by the cartilage of Wrisberg, which in this animal is wanting.

The hyoid apparatus consists, as usual in apes, only of the basi-hyal and of two thyro-hyals. The body of the bone is short and strongly curved upward as well as forward. Its breadth measured in a straight line from side to side is 2.4 cm. The thyro-hyals, which are connected by joints, measure, the right 4.2 cm., and the left 3.8 cm.

The two halves of the thyroid can be separated or approximated with such ease that a want of union was suspected, but a cross-cut at the angle showed that the cartilage is continuous. There is but a slight forward projection of the angle. The vertical length of this between the two notches is 2.2 cm. Both cornua bend strongly inward, especially the upper. The oblique line ends below in a very prominent tubercle which overhangs a deep fossa. The fibers of the crico-thyroid muscle are inserted into the lower border of the cartilage, the tubercle, the fossa behind it, and the inferior cornu. There is a suggestion of a separation into two layers described by Gratiolet and Alix The superior cornu is separated from the extremity of the great horn of the hyoid by a nodule (*cartilago triticea*) which touches both. The flexibility of the superior cornu is very striking.

The cricoid cartilage has not been uncovered, for it was thought best not to dissect the larynx. Its height in front is 7 mm. and behind 2.1 cm.

The arytenoids, for the same reason, are not accessible.

The true vocal cord is 2.3 cm. in length. Its delicacy has been described by others. It seems nothing more than a very thin fold of mucous membrane. The greatest distance between the true and false cords across the middle of the entrance of the ventricle is 5 mm.

The *ventricles and the roaring sac.* Each ventricle is prolonged upward behind the hyoid to the side of the epiglottis for more than 1 cm. from the superior cord. The left ventricle ends blindly. The right ventricle opens at its anterior part by an opening, which it is hard to see from the inside, into an anterior expansion. A rod 6 mm. in diameter, introduced from in front, fully distends the passage. I regret that I was not present when the roaring sac was opened by the primary incision at the autopsy. It was described as immense, extending over the front of the neck and the top of the chest outward as far as the coracoids. The portion still connected with the specimen passes up under the hyoid where it is sacculated. The communication with the larynx is just to the right of the median line.

THE TONGUE.

This organ seems hardly to have received the attention it deserves. It is longer and broader than in man. While strikingly similar, it presents some noteworthy differences. As in the human tongue the anterior two thirds of the dorsum are to be sharply distinguished from the posterior one, which has the *papillae circumvallatae* near its front and is occupied by adenoid tissue and mucous glands. In "Gumbo" the anterior two thirds besides the filiform papillae have very many fungiform ones, especially near the tip. What is remarkable is, that the characteristics of the dorsal mucous membrane are prolonged at the tip onto the inferior surface for 5 mm. or more. In the posterior third there is an oval swelling of the whole tongue in the middle, while in man there is a median furrow. The circumvallate papillae, some seven in number, are arranged rather like a T than a V. In some cases two papillae are surrounded by the same mote. The surface of the very posterior part is very irregular, owing to accumulations of adenoid tissue. Very striking is the large number of orifices looking like small pin-holes to the naked eye. Whether these are really the openings of large ducts or simply little cavities between adenoid collections can be determined only by the microscope. The papillae foliatae are more strongly developed than in man. These constitute a system of transversely placed ridges and furrows extending along either side of the tongue just in front of the end of the anterior pillar of the fauces. This system describes a marked curve with an inward convexity. From this in the anterior part of the posterior third of the tongue among the large papillae and somewhat in front of them is a curious system of curved raised lines suggesting that of the tips of the fingers.

THE CAECUM.

The caecum (pl. 8.) was the only part of the intestines saved. The vermiform process was divided some six inches from its origin, so that its length is not known. The caecum is not unlike a human one, being broader than long. It is a good example of Treve's third class, namely, that commonly found in man. It is very different from that figured by Gratiolet and Alix, which is long and tapering. A window cut in the dried and inflated specimen shows an ileo-caecal valve extending obliquely upward and outward from the inner side of the gut so as greatly to increase the size of that part of the intestine which must be called the caecum. The slit is 2.4 cm. long. The valve is continued about two thirds of the distance round the gut. Its greatest breadth is about 3 cm. Beneath it in the caecum, starting at the inner side from its under surface, is another smaller fold which diverges from it. This is best marked toward the posterior surface of the caecum. There is a small valve guarding the upper part of the entrance of the appendix.

The ascending colon is very large and strongly sacculated.

THE BRAIN.

According to agreement, the brain was so hardened as to make it fit for microscopic sections. The hemispheres were put at my disposal for the study of the convolutions. The length, after hardening, is 11.2 cm., the breadth, 9.4 cm., the height, 6.7 cm. Seen from the front there is a strong median downward projection of the frontal lobes where they rest on the cribriform plates. This keel is much greater than in "Sally," but perhaps a little less than in Benham's[1] figure of a common chimpanzee. The points which at first sight are most noteworthy and characteristic of this particular brain are the large size and diagrammatic appearance of the frontal and occipital convolutions in contrast to the small size and complication through small fissures of the parietal and temporal ones. There is a decided want of symmetry between the two halves.

Fissure of Sylvius. The main limb ends with a bifurcation on both sides of the brain. On the *left* side the anterior limb is easily recognized. It runs forward and ends in a bifurcation, the two parts of which make a slight concavity around a part of the third frontal, representing clearly enough the *pars triangularis*, Broca's promontory (pl. 9, fig. 1). In short, this is the Y plan often seen in the human brain, only the arms of the Y are short and widely opened. On the right there is no anterior limb at all, unless a depression on the third frontal in front of the praecentral fissure can count as a rudiment. This is precisely where the fissure should be. The little *subcentralis anterior* and the *praecentralis* are behind it and the *orbito-frontalis* in front of it. If the identification on the left side be correct, it will be observed that in front of the fissure of Rolando we find in order, first, the *anterior subcentralis*, then the *praecentralis*, then the anterior limb of the Sylvian, and finally the *fronto-orbitalis* (of Kükenthal and Ziehen[1]). The same series on the right is found by the interpretation offered above.

---

[1] A description of the cerebral convolutions of the chimpanzee known as Sally, [illegible] pl. 7.

Fissure of Rolando. Exceedingly plain and diagrammatic on the left, showing very clearly the two knees. The upper end opens on the mesial surface. The lower does not reach the Sylvian fissure. The same is essentially true of the *right* fissure, but the knees are less well marked. The fissure cuts the median line at a distance of about 6.5 cm. measured directly backward from a straight line at the front of the brain. The frontal lobe must be described separately on the two sides. The left is taken first, as more resembling the human brain. The anterior central convolution is much larger than the posterior. It is directly continuous with the three frontal convolutions, the first at the side of the median fissure, the second a little above the middle, and the third at the lower end. The middle convolution divides the praecentral fissure into a larger inferior and a smaller superior part. Each of these receives a *sulcus frontalis;* the superior is short, ending in a bifurcation; the inferior is long and complicated, running to the very front of the brain where it ends with a sweep inward. There is another fissure (? pl. 10, fig. 1) very like one described by Benham in "Sally" which also has its upper end internal to the *frontalis superior.* It is well marked and deep, with an external branch. It is not clear whether it is to be called a continuation of the *sulcus frontalis primus* or a *frontalis mesialis.* The second frontal convolution fuses with the first at the front of the brain. The third frontal convolution arises from the very lower end of the anterior central, runs at first upward, then, turning forward, it surrounds the bifurcated anterior limb of the Sylvian fissure, forming a rudimentary but distinct *pars triangularis.* In front of this, it rises again to loop round the *sulcus orbito-frontalis*, which is a striking fissure. The inferior or orbital surface of the frontal lobe is not easily understood. A small fissure running to the mesial surface must represent the olfactory fissure. The general direction of the other fissures is forward and inward. The *sulcus orbito-frontalis* bounds it externally but behind runs into its inferior surface.

The right frontal region is very different in some important respects. The anterior central convolution is larger than the left one, consequently its predominance over the posterior is more marked. The second frontal convolution is very large in its first part. The superior praecentral sulcus is longer than on the left. The superior frontal sulcus runs forward almost to the orbital border of the brain. This is a very uncommon development of this furrow which I do not remember to have seen equalled in any figure of a chimpanzee brain. The *sulcus praecentralis inferior* almost reaches the fissure of Sylvius. Owing to the [illegible] anterior limb of the fissure of Sylvius, the third frontal [illegible] has the shape of a solid wedge placed base downward [illegible] its surface which represents the anterior limb. It then winds over the *sulcus orbito-frontalis.* The second frontal fissure is interrupted by [illegible] between the second and third convolutions. On the inferior surface, the olfactory fissure does not run to the median line. There is a deep fissure in the posterior part of the orbital surface curving forward and outward, which has no representation on the left. The median surface of the frontal lobe is left to be taken later.

---

[1] Untersuchungen über die grosshirnfurchen der primaten. Jena. zeitschr., vol. 29, 1894.

The parietal lobe. The external parieto-occipital fissure, by which is meant that part of the internal one of the same name which extends into the convexity of the brain, is about 2 cm. long and similarly disposed in each hemisphere. It is surrounded by the *arcus parieto-occipitalis*, the classical *pli de passage*, which is quite uncovered by the *operculum*, but a little shut in anteriorly by the parietal lobe. The *sulcus occipitalis transversus* (Affenspalte), also symmetrical in the two halves, runs from the median line, just behind the *arcus* to the outer, lower, border of the hemisphere. In the first three quarters of its course it runs outward and slightly forward, then it bends strongly downward. The intra-parietal fissure is simple and nearly symmetrical. It consists of an inferior vertical part which is continuous with the main (horizontal) portion which runs into the Affenspalte just below the *arcus*. The superior vertical part is distinct. It can be called "vertical" only by homology, for it is decidedly more horizontal. The main limb just before entering the Affenspalte sends off a small branch which runs just in front of the arcus toward the median line.

The posterior central convolution is small. On the right it is evidently continuous along the whole length of the fissure of Rolando. It is continuous also on the left, though less evidently, for it is nearly cut through at the two knees of the fissure of Rolando above by the upper detached portion of the intra-parietal fissure, and below by a sulcus from the main stem. At the lower end this convolution expands on the left side into a triangular mass with a central imprint, probably representing the *sulcus subcentralis posterior.* The superior parietal convolution consists of two gyri separated in front by the upper part of the intra-parietal fissure which is here essentially horizontal. They unite behind it and are continued into the parieto-occipital arcus, bounding the fissure of that name, which is quite uncovered by the operculum.

The inferior parietal convolution divides into the supra-marginal gyrus surrounding the fissure of Sylvius and the angular gyrus which descends to the edge of the hemisphere and then, rising sharply, is continued as the second temporal convolution. This applies to both sides.

The temporal lobe, so far as seen on the outside, requires little description. The parallel fissure below the first temporal convolution is, as seems always to be the case in the chimpanzee and in all the higher primates, remarkably clear and simple. It ends above with a bifurcation, around the lower branch of which the angular gyrus has to turn to reach the second temporal convolution as just described. The first temporal convolution is self evident. The second and third seem to be somewhat fused on both sides. Those on the under surface of the lobe will be considered later.

The occipital lobe, as seen externally, is marked by the large size and extreme simplicity of its convolutions. It looks like an undifferentiated mass on which a capital Y has been imprinted, lying on its side with the stem forward. This is the *s. occipitalis obliquus.*

The *gyrus occipitalis secundus* (the operculum) lies behind the Affenspalte and joins the angular gyrus; before doing so, however, it is itself joined by the third occipital which lies under the Y. Beneath this runs the *sulcus occipitalis inferior* just above the lower edge of the hemisphere. This fissure is well marked on both sides, giving off a vertical ascending branch, round which the second temporal convolution turns. On the right the middle part of this fissure is not visible from the side.

The median surface of the brain and the inferior aspect of the occipital and temporal lobes remain to be described. The *fissura calloso-marginalis* is very simple and so like that of the human brain that detailed description is needless. It begins on the right hemisphere far back on the mesial surface of the frontal lobe, and is uninterrupted. On the left the plan is much like that figured by Kükenthal and Ziehen. There is below a *sulcus rostralis* with which the *calloso-marginalis* is joined by a little fissure so minute and shallow that the junction is more apparent than real. Behind its termination is the *lobulus quadratus* which is connected with the *arcus parieto-occipitalis* above and with the *gyrus fornicatus* below. The last named convolution and its continuation, the *gyrus hypocampi*, are uninterrupted on the right. On the left it is divided by the *fissura calcarina.* The *uncus* is well marked.

The internal parieto-occipital fissure is similar on both sides. Seen from the mesial surface, it appears to split above into two parts. The posterior one is the true fissure, being continued out into the convexity as above described. The anterior branch just passes the upper border of the hemisphere. The *gyrus intercuneatus* is made out by separating the parts as far as possible. It is quite hidden, being very deeply placed. Should it rise to the surface, it would separate the internal parieto-occipital fissure from the external, making the former end anteriorly to the latter, as Benham has shown. The lower end of this fissure divides into two small branches which connect with no other fissure. In the right hemisphere the posterior division cuts through the gyrus separating it from the calcarine fissure.

The calcarine fissure differs in one important respect in the two sides. In both it ends in a fork very near the hind end of the brain. On the left it opens into the fissura *hypocampi;* on the right it joins what seems to be a peculiar collateral fissure. A deep fissure is seen in the cuneus, which, according to Kükenthal and Ziehen, is very constant in the chimpanzee. On the left the cuneus sends a convolution to the gyrus hypocampi just above the end of the calcarine fissure; on the right, owing to the peculiarity of the calcarine fissure, this gyrus seems to run more directly into the *gyrus hypocampi.*

The under side of the temporal lobe presents a very different appearance in its anterior half, which is frankly inferior, and in the posterior portion, which slants into the oblique inferior occipital surface. The former shows large simple convolutions. The latter is broken up by many secondary sulci. The former shows the ends of the first and second temporal convolutions passing obliquely forward from the outside of the brain and behind them the third which is quite plain on the under surface of the left half, but not clear on the right. The left collateral fissure is perhaps best described as splitting posteriorly into two parallel divisions. The *lobulus lingualis* lies between the inner of these divisions and the *fissura calcarina.* The *lobulus fusiformis* is between the two divisions.

On the right the *fissura calcarina* runs obliquely outward across the under surface of the temporal lobe to end in a short fissure which represents the separated anterior portion of *fissura collateralis.* The posterior part of this fissure is in its proper place. The *lobulus lingualis* is cut off by the abnormal direction of the *fissura calcarina.* The arrangement is, so far as I know, an undescribed one.

EXPLANATION OF THE PLATES

PLATE 7.

Fig. 1. Foot.
Fig. 2. Hand

PLATE 8.

Fig. 1. Caecum. The appendix runs along the lower edge to the left of the [illegible]
Fig. 2. Inside of caecum. The ileo-caecal valve is seen above. Below [illegible] lower the opening of the appendix
Fig. 3. The upper end of the left femur, showing a small [illegible]

PLATE 9.

Fig. 1. The outer surface of the left hemisphere of the brain.
Fig. 2. The outer surface of the right hemisphere of the brain.

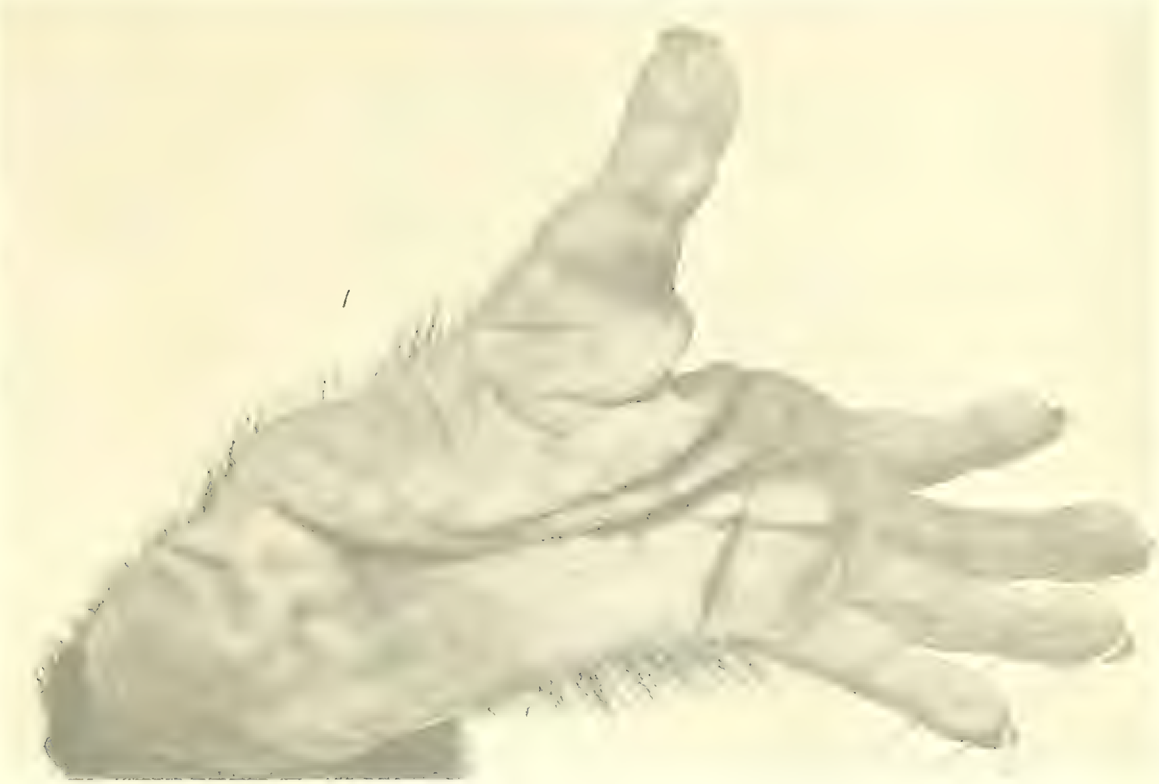
PLATE 10.

Fig. 1. The brain seen from above.
Fig. 2. Inner aspect of the right hemisphere.

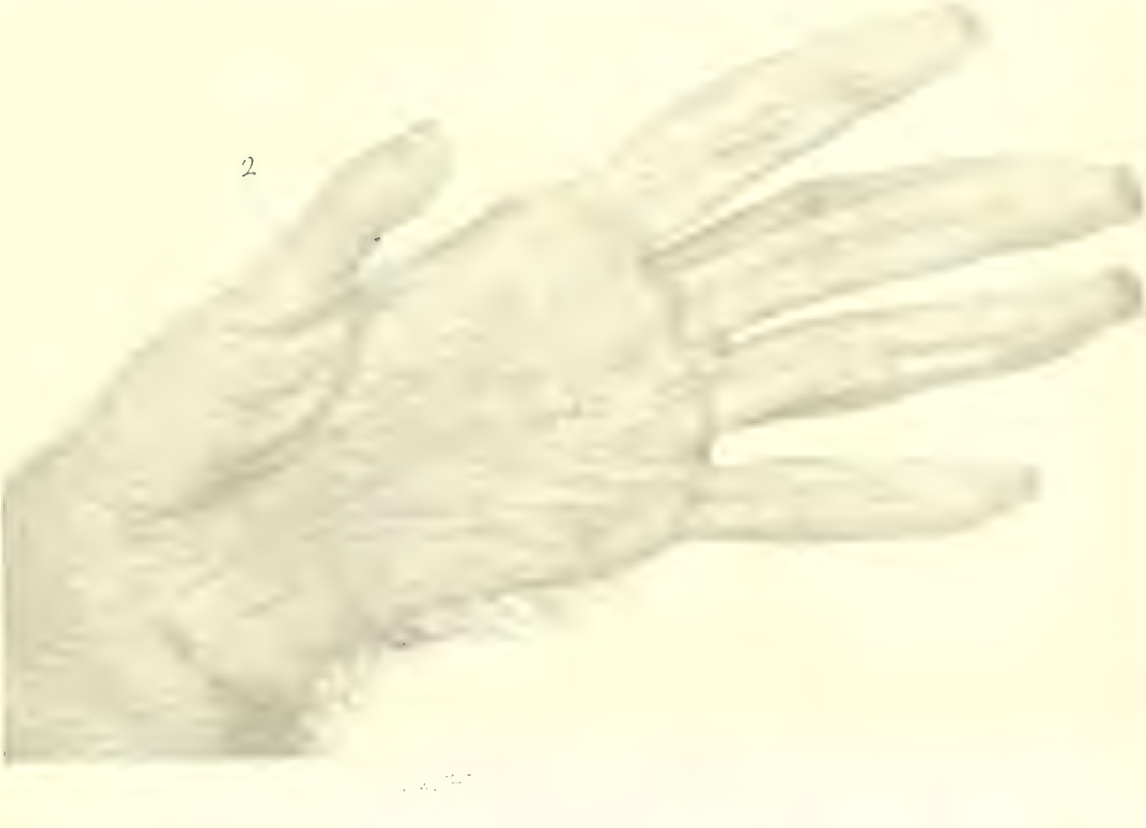
LETTERING USED IN PLATES 9 AND 10.

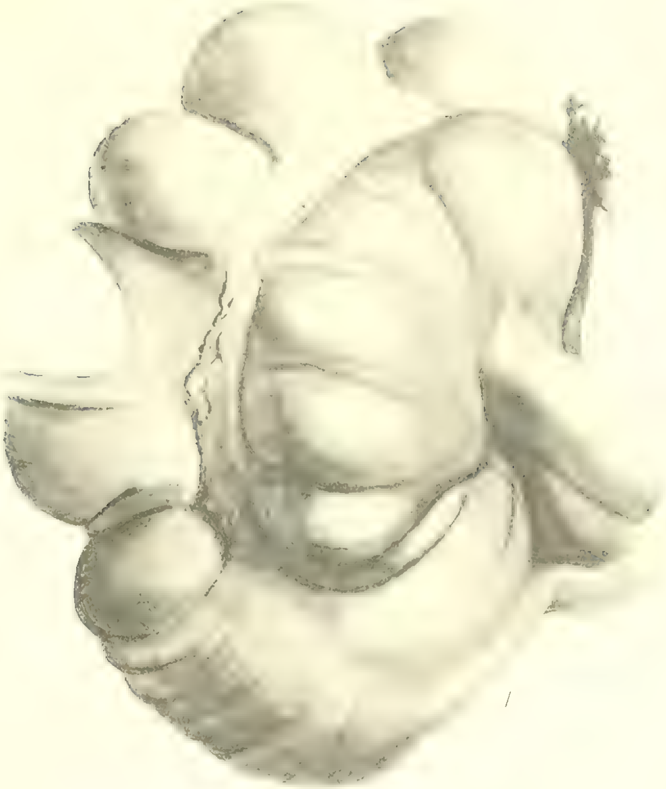
af. Affenspalte: sulcus occipitalis transversus
fc. Fissura calcarina.
f. coll. Fissura collateralis.
f. p. o. Fissura parieto occipitalis
f. po. ext. Fissura parieto-occipitalis externa.
f. R. Fissure of Rolando: fissura centralis.
r. asc. f. s. Ramus ascendens, vel anterior, fissurae Sylvii
s. c. m. Sulcus calloso-marginalis.
s. i. p. Sulcus intra-parietalis.
s. oc. ob. Sulcus occipitalis obliquus.
s. o. f. Sulcus orbito-frontalis.
s. o. i. Sulcus occipitalis inferior.
s. pc. i. Sulcus praecentralis inferior.
s. pc. s. in plate 10 should be r. s. i. p. for the separated superior branch of the intraparietal fissure.
s. sub. c. a. Sulcus subcentralis anterior.
s. sub. c. p. Sulcus subcentralis posterior.
? Vide page 48.

1

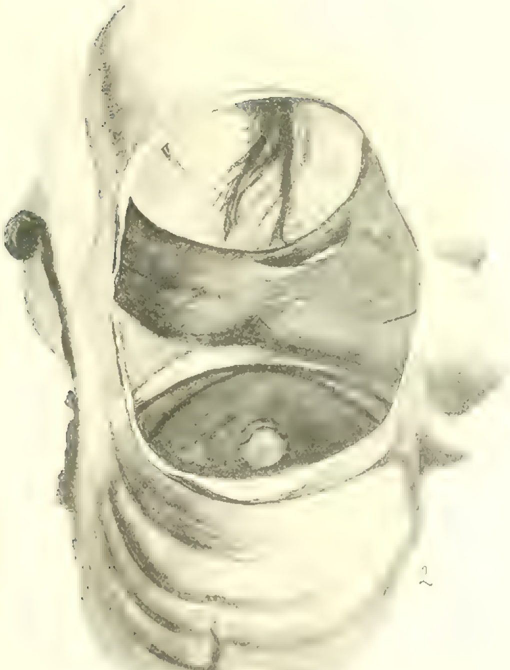


2

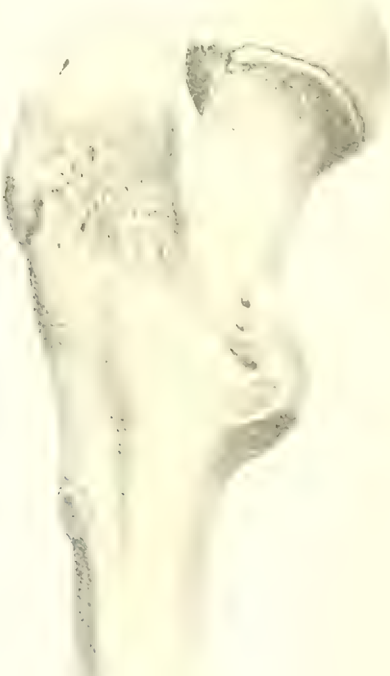


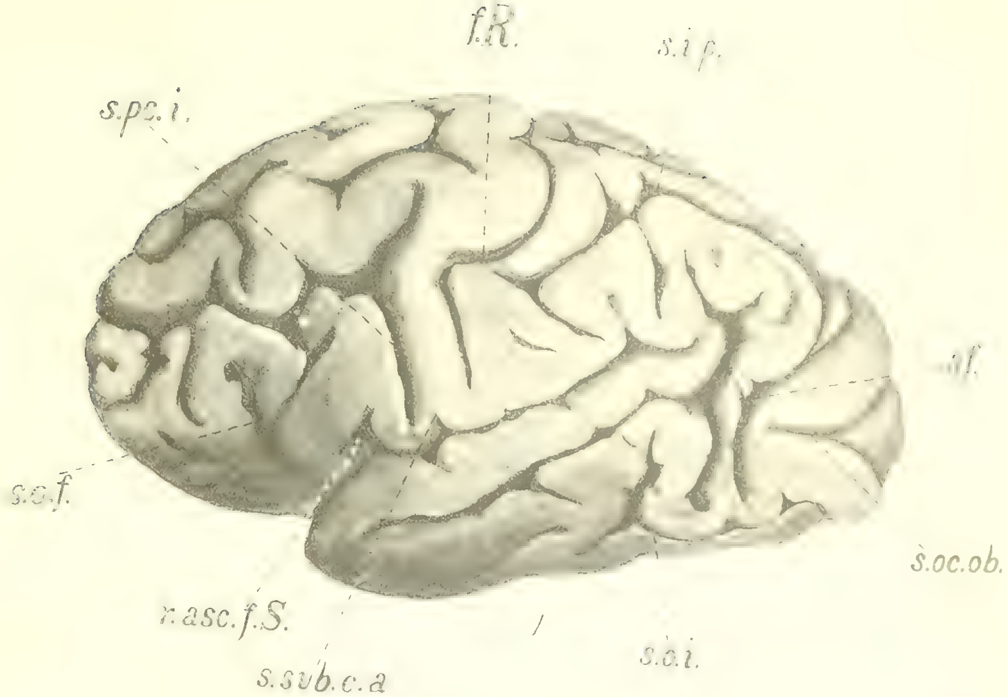


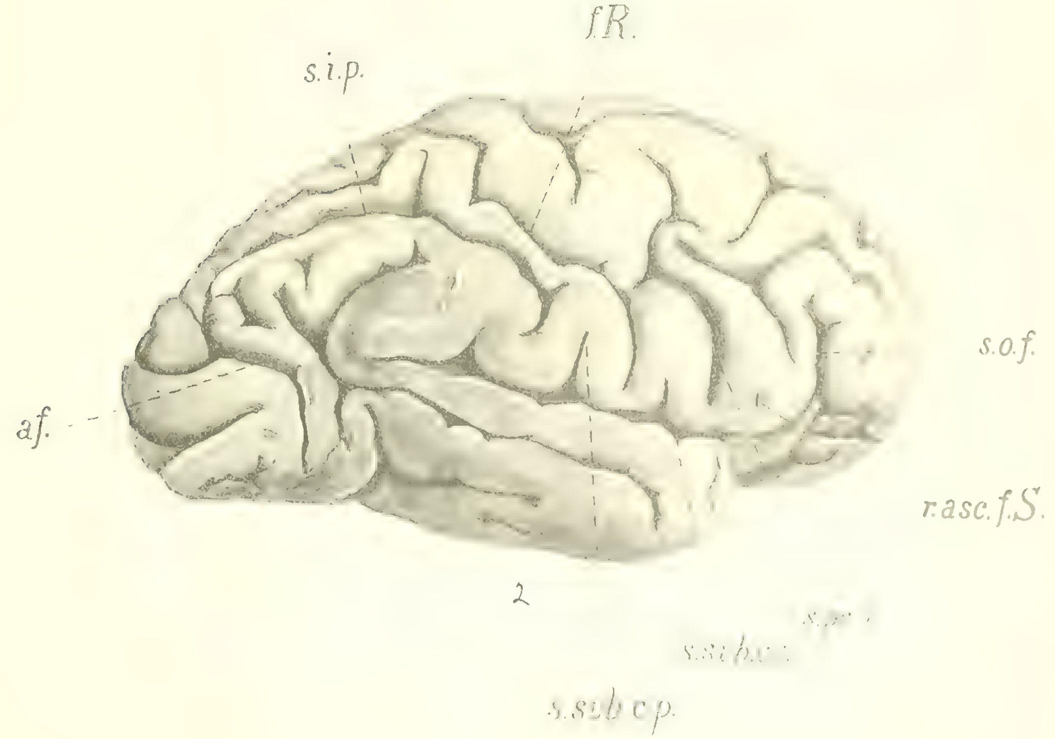
1



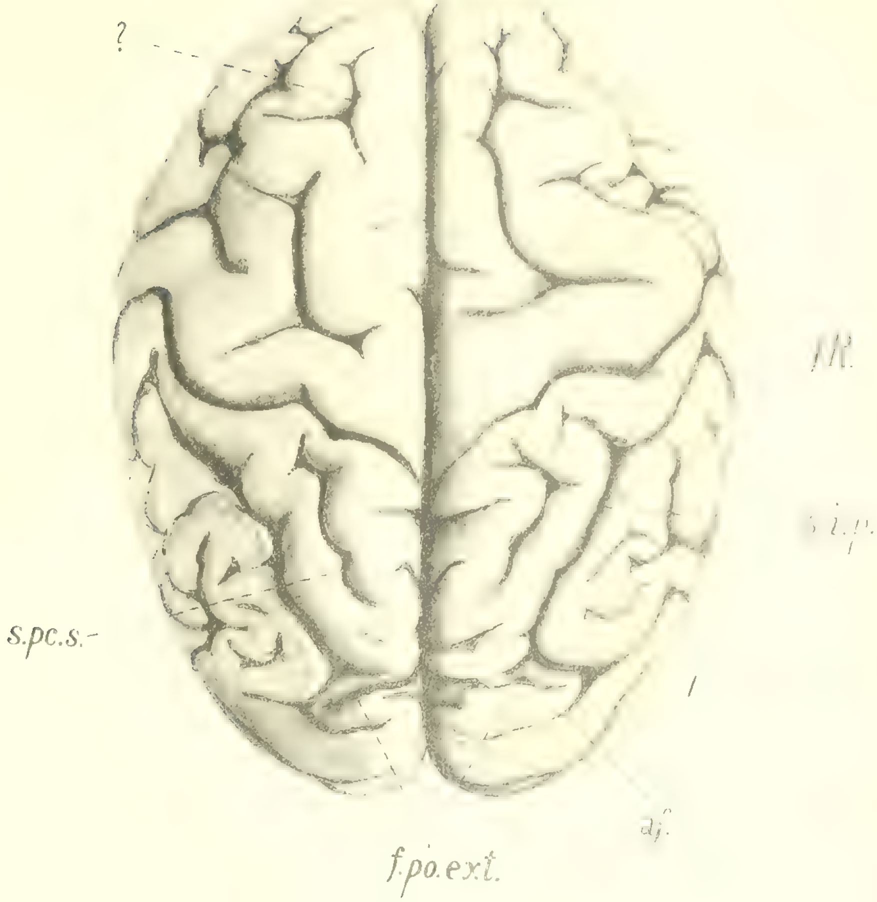
2

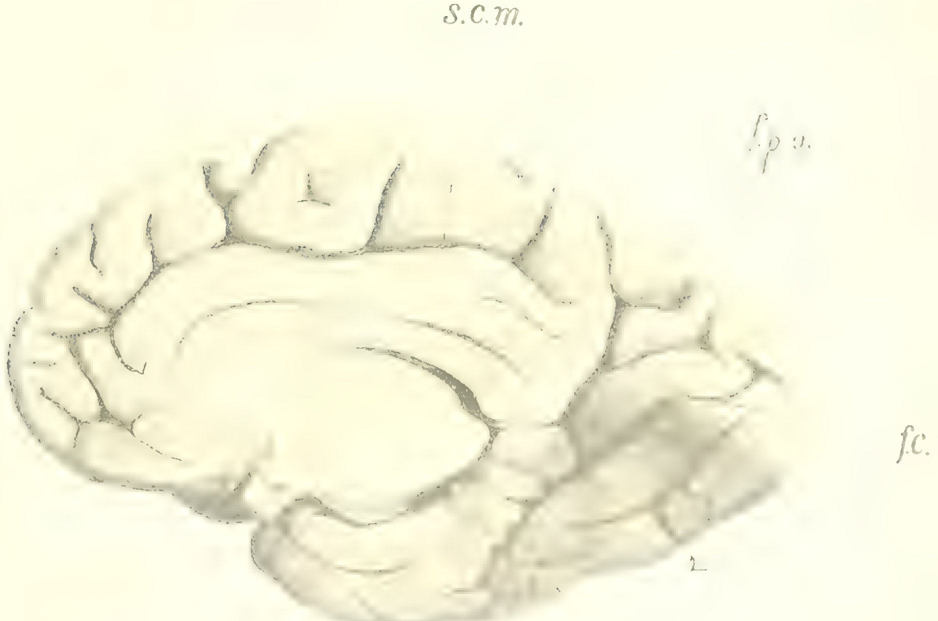



f.R.
s.i.p.
s.pc.i.
a.f.
s.o.f.
s.oc.ob.
r.asc.f.S.
s.o.i.
s.sub.c.a


f.R.
s.i.p.
s.o.f.
af.
r.asc.f.S.
s.pc.i.
s.sub.c.a.
s.sub.c.p.

2


?
fR.
s.i.p.
s.pc.s.
l
af.
f.po.ext.


s.c.m.
f.p.o.
f.c.
2
f.coll.

3. SYNAPTA VIVIPARA: A CONTRIBUTION TO THE MORPHOLOGY OF ECHINODERMS.

BY HUBERT LYMAN CLARK.

(Read November 3, 189[illegible].)

CONTENTS.

1. Introductory 53
2. History and systematic position of Synapta vivipara 54
3. Distribution and habits 55
4. Fertilization and segmentation of the egg 58
5. Gastrulation and formation of the hydrocoel and coelomic vesicles 61
6. The development of the [illegible] [illegible]
7. The development of the adult Synapta [illegible]
8. The anatomy of the adult [illegible]
9. Conclusions [illegible]
10. Literature [illegible]
11. Explanation of plates [illegible]

1. INTRODUCTORY.

In February, 1896, through the kindness of Dr. W. K. Brooks, there were placed in my hands for study a number of specimens of a small brown Synapta from Jamaica. In their body-cavities there were numerous young ones in all stages of development, so that an excellent opportunity was offered for working out the embryology. So interesting did this prove that I gladly availed myself of the privilege of spending the months of May, June, and July, 1896, at Port Henderson, Jamaica, in the marine biological laboratory of the Johns Hopkins University. For such a privilege I am under the greatest obligations to the authorities of that institution. During those months, I studied the segmentation of the egg and the early stages of development from living material and obtained an abundance of preserved material for further investigations. Since my return I have been engaged in a detailed study of the development and anatomy of the animal under the direction of Dr. Brooks, and it gives me great pleasure to acknowledge the debt I am under to him for his suggestions and help.

The young were easily procured by cutting off the heads of the adults and thus setting free the contents of the body-cavity. They could then be killed as desired, but young taken from the body-cavities of preserved adults were fully as satisfactory for all purposes. The best results were obtained by the use as a fixing agent of "corrosive-acetic" (four parts corrosive-sublimate and one part glacial acetic acid), but excellent preservation, especially for the adults, was secured by the use of picro-sulphuric or picronitric acid. Corrosive-sublimate alone gave poor results, while Perenyi's fluid proved very unsatisfactory, the material prepared with it showing only fair preservation, and staining very poorly. Very good material for the study of the calcareous bodies and the development of the calcareous ring was obtained by the use of absolute alcohol. In staining, it was found useless to try any solution which contained less than seventy per cent alcohol, collapse and distortion of the tissues always resulting. Kleinenberg's haematoxylin and eosin gave good results, but acid borax-carmine (70% alcohol) and Lyons blue (70% alcohol) proved the most satisfactory. The early stages of the larvae were oriented and imbedded in celloiden before imbedding in paraffine, and thus kept their shape very well. Although material was so abundant and easily obtained, it is impossible to tell the age of the different embryos, for none of the eggs obtained developed beyond the blastula, and later stages would live outside of the mother for only a very short time. Accordingly it cannot be determined how many days or weeks are required for the growth of the pentactula or older stages, though there is reason to believe that growth, at least early in life, is very rapid.

2. History and Systematic Position of Synapta vivipara.

The Danish naturalist Orsted ('50) mentioned the discovery in the West Indies of a new genus of the Synaptidae, the chief characteristic of which was its being viviparous. To this genus he gave the name *Synaptula*, and the type species he called *vivipara*. In his very brief and unsatisfactory account, for which I am indebted to Ludwig's German translation ('81), he mentions the occurrence of the form in "shallow-water," describes the color as "greenish," and speaks of the presence of "eyes," "skin-glands," and "anchors." He never published anything further in regard to the species, and later writers, as Bronn ('60), Selenka ('67), and Semper ('68), accepted the genus *Synaptula* without comment. But Ludwig ('81), in describing a viviparous Chirodota (*C. rotifera*) from the coast of Brazil, suggested that it might be the species on which Örsted had based his new genus. This conclusion was adopted by Lampert ('85), and in his work we find *Synaptula vivipara* given as a synonym under *hirodota rotifera*. Théel ('86) placed *Synaptula vivipara* in the list of Synaptidae about which little or nothing is known, but he suggests in agreement with Ludwig ('81) that the stage of development which the eggs reach before leaving the mother, is not a satisfactory character upon which to base a new genus. Ludwig ('86) described a small *Synapta*, found in floating seaweed, west of the Abrolhos Reef, Brazil, which he regarded as identical with Örsted's species, since it contained young in the body-cavity and answered Örsted's description, except in color

In 1891, students of the Johns Hopkins University found at Port Royal, Jamaica, a viviparous Synapta, and, in 1893, another party from the same University brought back a large amount of preserved material of this species, which they found abundantly about Port Royal. It was this material which came into my hands, and after examining it and studying the living animal at Port Royal, I had no difficulty in satisfying myself that it, as well as Ludwig's Abrolhos specimen, was indeed Orsted's *Synaptula vivipara*. A brief description to establish its position in the genus Synapta, was published by Clark ('96), and attention was there called to its similarity to *S. picta* Théel ('96). This species was described from a single specimen in the Challenger collection, from Bermuda, and the agreement of all its characters with those of *S. vivipara* was very striking. Dr. Théel writes me that he has specimens of a viviparous Synapta from Bermuda in his hands at the present time, which agree with *S. picta* and *S. vivipara* so completely that he has no doubt that all three are the same species; but the evidence is incomplete, owing to the absence of the anchors and plates in his Bermuda specimens, caused by the killing agent used. Although, as we shall see, *Synapta vivipara* differs in several important particulars from all other Synaptas hitherto described, they are not sufficiently obvious to warrant its separation, under the existing classification of the Synaptidae, as a distinct genus. Synaptula must therefore become a synonym of Synapta, and the synonomy of *S. vivipara* will be as follows: —

Synapta vivipara (Orst.) Ludw. Zool. Jahrbücher. Bd. 2, p. 28. 1886.
Synaptula vivipara Orsted. Vid. med. fra d. nat. For. i Kjöbenhavn for 1849–50, p. vii.
Synaptula vivipara Bronn. Klas. und Ord. d. Thier., Bd. 2, p. 403. 1860.
Synaptula vivipara Selenka. Zeit. für wiss. Zool., Bd. 17, p. 365. 1867.
Synaptula vivipara Semper. Reis. in Arch. Phil., 2. Theil, 1. Bd., p. 24. 1868.
Chirodota rotifera (in part only) Lampert. Die Seewalzen. Wiesbaden. 1885.
Synaptula vivipara Théel. Report on the Holothurioidea. "Challenger" Reports. Zool., Vol. 14, p. 32. 1886.
Synapta picta Théel., p. 10. Report on the Holothurioidea. "Challenger" Reports. Zool., Vol. 14, p. 32. 1886.

3. Distribution and Habits.

Örsted's specimens of *Synapta vivipara*, he tells us, were from the West Indies, and all of the specimens I have seen, came from Jamaica. Ludwig's single specimen came from the Abrolhos Reef off the coast of Brazil (18° S. lat.), while all of Théel's specimens are from Bermuda (32° N. lat.). We may therefore conclude that the species is pretty widely distributed throughout the eastern Atlantic ocean, wherever suitable conditions are found. In Jamaica, however, the species is extremely local and was found in only one place, the so-called "lakes" at Port Royal. These "lakes" are parts of the harbor which have been wholly or in part cut off by the growth of mangroves, so that they are very quiet bodies of water, though not at all stagnant or brackish. On the roots of the mangroves, which hang down in the water on all sides, is an abundant growth of vegetable and animal life. In some places, a particular sea-weed. one of the Florideae, crowds out all the other Algae. In this weed *Synapta vivipara* makes its home, and though carefully looked for elsewhere, it was found in numbers only in such situations. The late Dr. J. E. Humphrey kindly identified this alga for me, as *Acanthophora thierii* Lamouroux. This weed also grows in large bunches on the bottom in the shallow water of the harbor just outside the "lakes," and I was told that in 1893 the Synapta was found in great quantities there, but in 1896 it seemed to have entirely disappeared from that place. At Montego Bay, on the northwest coast of Jamaica, Acanthophora is very abundant on the mangrove roots, but a thorough search revealed no sign of Synaptas there. Even in the Port Royal "lakes," their distribution was very capricious, and only certain favored masses of Acanthophora contained them in any numbers. They seem to be quite social in their habits, and usually if one or two were found, there would be a whole colony of them. They are very sensitive to changed conditions, and I was unable to keep them alive in aquaria more than twenty-four hours. The anchors in the body-wall are so abundant and prominent that they cling very tenaciously to anything with which they come in contact, especially the hands, and it is accordingly no easy task to disentangle them from the sea-weed without injury. They seem to be able to swim very little, and it is doubtful if they ever leave the bunch of sea-weed, in which they have once settled. Their food consists largely of vegetable matter, diatoms being abundant in the stomach, but probably many small crustaceans and worms are also eaten. The tentacles are kept constantly in motion, and it was very common to find small amphipods caught among them, but I was unable to find evidence that these crustaceans ever served as food. Semon ('87) has called attention to what he considers a mimicry of coloration in *Synapta inhaerans*, in relation to the bottom on which it is found. In this connection, it is interesting to note that the reddish and greenish brown shades of *S. vivipara* are almost exactly those of the Acanthophora in which it lives. So close is the resemblance that it is very easy to overlook Synaptas, even when the sea-weed is in one's hand. Whether this coloration is actually protective or not is doubtful, for they seem to have few, if any, enemies. No internal parasites were observed; externally however a small brown calcareous sponge, like Grantia, was found firmly attached to the skin, just behind the circle of tentacles. When placed in aquaria the Synapta does not break up by muscular contractions, like S. *inhaerens*, nor does it ordinarily eviscerate like many holothurians, but after crawling about restlessly for a while, it stretches out on the bottom and dies, almost without the contraction of a muscle. In a few cases, evisceration at the mouth took place, when they were thrown into a killing agent.

Breeding goes on all through the spring and summer ; and there is no evidence to show that it does not go on all the year round. My earliest specimens, collected April 30, contained many well-developed young, and up to the end of July in all the specimens obtained, young were found, while Ludwig's specimen from Abrolhos was collected in September and contained very young embryos. The number of young in the body-cavity of a single adult varies greatly, depending more or less on the size of the individual. Specimens not over a centimeter long may contain a few, while some very large ones have scores. The largest number I have found is 176. It is a curious fact that the young are almost always in two broods ; that is, a certain proportion of them will all have reached a given age, say that of the pentactula, while the remainder will be much younger, say about that of the gastrula. When the young are very few, they will all be the same age, while if they are very numerous, they will sometimes show *three* different stages. This fact seems to indicate that the eggs ripen and pass into the body-cavity in lots of from six to a hundred, and that several days elapse before another lot is ripened. Regarding the length of time during which the young remain in the body-cavity, it is impossible to make even an estimate. Animals kept in aquaria frequently gave birth to young only five mm. long, and it was not usual to find much larger specimens in the adults examined, but sometimes a young one, fifteen or twenty mm. long, with all the characters of the adult, would be found still inside its mother. Observations made on the living animals showed that birth occurs normally at the posterior end of the body, apparently through the anus. Investigation showed that this was accomplished by a rupture of the body-wall, which may be through the skin some little distance from the anus (Fig. 29), or, as seems to be more generally the case, through the wall of the rectum close to the point where it joins the external body-wall, the young passing out through the anal opening. It may be that the openings in the wall of the rectum (Figs. 30 and 31), to be described later, are concerned in the birth of the young, but they seem to be too small to be of any service in this connection, except possibly as starting points for the rupture of the rectum wall. Under abnormal conditions, I found by experiment, rupture of the body-wall and consequent birth of the young may occur at other points than near the anus.

4. Fertilization and Segmentation of the Egg.

Like all other known Synaptas, *S. vivipara* is hermaphroditic. Ripe spermatozoa and ova are found in the same genital organ and even in the same branch, and to judge both from living material and preserved specimens, even at the same time; but this latter point could not be proven since it is impossible to determine simply by observation, when the egg is mature. The branches of the genital gland are nile-green in color in the living animal, while the fully grown ova are brownish yellow, and the spermatozoa, when in any quantity, appear to be white. In shape, the latter are like those figured by Jourdan ('83) for *Holothuria tubulosa.* The mature egg (Fig. 1) is about 200μ in diameter and before fertilization is not provided with any membrane. It is full of yolk material but comparatively transparent, so that the internal changes could be watched up to a late stage of development. Artificial fertilization proved unsuccessful, although attempted several times. Whether self-fertilization takes place or not could not be positively decided, but that it is at least very improbable seems clear from the structure of the genital organs and the probable manner of egg-laying. The genital gland of the adult Synapta lies just above the oesophagus, with one or two branches on each side of the dorsal mesentery and with the genital duct lying in that mesentery and opening to the exterior close to the base of one of the mid-dorsal tentacles. A cross-section of one of the branches (Fig. 40) shows that it consists of an external covering, the continuation of the epithelium, a very scanty connective-tissue layer consisting only of a few scattered mesenchyme cells, and a much folded germinal epithelium surrounding the lumen of the gland. Of the layer of circular muscle fibers which was found in the genital gland of *S. digitata* and *S. inhaerans* by Quatrefages ('42), Baur ('64), and Hamann ('84), I have found no trace in *S. vivipara.* The branches of the gland contract vigorously after being cut from the body, but so far as I could see, these contractions were always longitudinal. The germinal epithelium is more or less plainly made up of two or more layers of cells of which the external are the larger. As will be seen from figures 39 and 40, from this external layer of cells the ova arise and so come to lie between the germinal epithelium and the epithelium of the body-cavity, and do not pass into the lumen of the gland at all. This arrangement is quite the reverse of what Cuénot ('91) has shown to exist in *S. inhaerans*, and gives us a clue as to how the eggs get into the body-cavity of the mother. When the eggs are mature, they press so closely against the external epithelium of the gland that it bulges out sufficiently to be seen with the naked eye, in the living gland. Sections show that the epithelium over such ova is so stretched as to be thinner than elsewhere (Fig. 39), and probably the eggs enter the body-cavity simply by the rupture of the epithelium at that point. While this has never been actually observed, the theory is supported by a further examination of the genital gland. The smaller internal cells of the germinal epithelium give rise to spermatozoa, which are almost invariably to be found in the lumen of the gland, never on the outside with the ova. If we trace the lumen forward we find it passes directly into the lumen of the genital duct, the internal walls of the latter actually being formed by a continuation of the germinal epithelium, which has become of uniform thickness and ciliated internally (Figs. 36 and 37). The lumina of the two or three branches of the gland unite on entering the duct (Fig. 36) and pass through the latter upwards towards the body-wall. At no point is there any sign of communication between the genital duct and the space external to the germinal epithelium in which the ova lie. If we follow the genital duct upwards to where it comes in contact with the body-wall, we find it does not fuse with the ectoderm and open at once to the exterior, but simply lies in the connective tissue with its end against the ectoderm (Fig. 38), and although there are probably openings through which the spermatozoa pass out, they are so extremely small I have not been able to demonstrate them satisfactorily. In nearly all the specimens examined the genital duct contained large quantities of spermatozoa, but in no case was there any trace of an ovum. That the openings at the end of the duct are not directly continuous with openings through the body-wall is indicated by the occurrence of spermatozoa, sometimes in large quantities, in the connective tissue surrounding the terminus of the duct (Fig. 38). From all these facts I am convinced that the ova pass into the body-cavity by a rupture of the peritoneal epithelium, while the spermatozoa pass outward through the genital duct to the exterior. In *Cucumaria glacialis*, the only other viviparous holothurian concerning whose breeding we have any information, Mortensen ('94) thinks the eggs are laid on the bottom and taken up afterwards into the brood-sacks of the mother. But it is manifestly impossible that the eggs of *S. vivipara* could get into the body-cavity in any such way. The next question that arises is, how do the spermatozoa reach the ova inside the body-cavity of the mother, and the answer brings to light another interesting modification of structure, adapted to the viviparous habit. Careful examination of the rectum shows that through its wall there are direct channels of communication between the body-cavity and the exterior through the anus. The wall of the rectum is folded and ridged longitudinally, and at certain places, parts of these ridges have pushed out and fused with invaginations from the surrounding coelomic wall, forming distinct tubes connecting the interior of the rectum with the interior of the coelom (Figs. 30 and 31). No trace of valves or cilia was found in any of these tubes, but the passage of water in and out could be easily regulated by the opening and closing of the anus. With the anus open, each muscular contraction of the animal would tend to either force water out or draw it in through these openings, and in that way spermatozoa could easily get into the body-cavity and thus fertilization could take place within. This will appear more probable when it is remembered that the animals are very social, and that the water around a mangrove root on which there are hundreds of them, must contain countless spermatozoa. There is also a possibility that spermatozoa enter the body-cavity, through the water-pore and stone-canal, which, as we shall see, remain open in the adult, and also open into the body-cavity.

After fertilization a membrane forms around the egg and segmentation begins. It seems probable that the extrusion of the polar bodies occurs before the formation of this membrane, as Selenka ('83) found no trace of them in the segmenting eggs of *S. digitata*, and I could not find them in any of the eggs of *S. vivipara* which I examined, although they were looked for with special care. Segmentation and the formation of the blastula occur in practically the same manner as has been so well figured by Selenka ('83) for *S. digitata.* The first plane of division forms two blastomeres of equal size and appearance (Fig. 2). After a resting period of about twenty minutes, the second plane of division occurs at right angles to the first, giving rise to four similar blastomeres (Fig. 3). The third plane is at right angles to the first two, and we now have an embryo of eight equal cells with a segmentation-cavity between them (Fig. 4). The sixteen-cell stage (Fig. 5) soon follows, the division plane being at right angles to the preceding. The appearance of the embryo at this stage is very peculiar and characteristic, the cells being arranged in a band or ring and the segmentation-cavity being open at each pole. Another plane of division, again at right angles to the preceding, doubles the width of the band and decreases the openings at the poles, but it does not divide the cells exactly equally, so that the upper- and lowermost rows are of somewhat smaller cells than the two middle rows and have a less diameter (Fig. 6 and 7). The subsequent divisions occur with a fair degree of regularity in alternating planes, each division decreasing the openings at the poles until at last they are entirely closed. This occurs when the embryo consists of approximately 256 cells, and so the blastula is formed (Fig. 8). The cells of the four equatorial rows are somewhat larger than the rest, but the difference is not at all noticeable and apparently has no significance. The divisions have followed on each other with great rapidity so that the complete blastula is formed after about four hours, while in *S. digitata,* according to Selenka ('83), the blastula is the result of twelve hours' growth. It is for this reason, that I am inclined to think that the whole process of development in *S. vivipara* is very rapid.

5. GASTRULATION AND FORMATION OF THE HYDROCOEL AND COELOMIC VESICLES.

Invagination of one of the poles of the blastula soon forms the archenteron from the blind end of which the mesenchyme cells now begin to arise, some of the endodermal cells being simply crowded out into the segmentation-cavity. I could find no evidence at all of Selenka's ('83) two primitive mesenchyme cells, but on the contrary, I found cells all over the archenteron which were in various stages of passing into the segmentation cavity. On the other hand in not a single case were there found any of the ectoderma-cells forming mesenchyme, and I feel no hesitation in affirming that the mesenchymel arises exclusively from the endodermal cells, contrary to Ludwig's ('91) observations on Cucumaria. The number of mesenchyme cells is comparatively small, and they never become so numerous or play so important a part in larval structures as they do in *S. digitata*, judging from Semon's ('88) account and figures. The completed gastrula (Fig. 9) is covered with cilia which are easily seen in the living specimens, but in none of my preserved material has it been possible to demonstrate them. In a few cases gastrula were found free from the egg-membrane and moving about actively in the fluid of the body-cavity, but the great majority are still enclosed in the membrane within which they rotate by means of the cilia. The membrane may be retained, as preserved specimens show, until long after the coelomic vesicles are formed, and I am inclined to believe that there is no definite time when it is cast off, but that it ruptures and is lost whenever the larva has grown too big for it. As the archenteron increases in length it bends to one side and unites with the wall of what subsequently becomes the dorsal surface of the larva. Its lumen breaks through the surface, and thus the water-pore is formed, as described by Selenka ('83) for *S. digitata*. Meanwhile the gastrula loses its spherical shape and becomes more or less elongated (Fig. 10). The cells at the end opposite the blastopore are already somewhat different in form from those elsewhere and make a sort of plate of thickened ectoderm (Fig. 21) which may correspond to the so-called "neural plate" of other echinoderm larvae. This plate, however, does not lie exactly opposite the blastopore, but somewhat toward the ventral side of the larva, and as the gastrula increases in length, it comes to lie more and more on that side. At the same time, the archenteron continues to increase in length and grows forward and at the same time ventralward, thus drawing away from the water-pore. In so doing, that part of it which grows forward pushes by the part opening through the water-pore, on the right-hand side (looked at from the dorsal surface) so that the latter comes to lie on the left side of the larva (Figs. 11 and 12). As the archenteron grows it completely severs its connection with this vesicle, and pushing onward and downward against the thickened part of the ectoderm, becomes attached to it, and the mouth breaks through at that point. The mouth may be formed before the separation between the archenteron and the other vesicle is completed. Meanwhile the latter increases in size, and its walls become thinner. It grows backward toward the blastopore especially and soon becomes constricted and divided into two vesicles, the anterior of which is connected with the exterior by the water-pore, while the posterior is entirely closed and lies beside the posterior part of the stomach, if we may so designate the middle section of the archenteron (Fig. 13). Soon afterwards this posterior vesicle grows out laterally to the right, across the dorsal surface of the larval hind-gut, and forms on the right-hand side a vesicle like itself, which soon becomes entirely separate from it (Fig. 14). The anterior of these three vesicles is the rudimentary hydrocoel, while the pair of posterior pouches represent the right and left coelomic vesicles. Their mode of formation is essentially the same as that described by Selenka ('83) for *S. digitata*, but the relative size of the various organs is markedly different, so that the figures of the same stages show almost no resemblance. If figure 15 of *Synapta vivipara* be compared with the auricularia of about the same age which Semon ('88, Plate 6, Fig. 2) figures, this difference will appear in many ways. The rudiments of the two coelomic pouches and especially of the hydrocoel are very much larger relatively in *S. vivipara* than in *S. digitata*, while the difference in the digestive tract is even more noticeable. In the European species there is a well-marked differentiation into fore-, mid-, and hind-gut, while in the Jamaican form there is no such distinction evident. A remarkable difference is also to be seen in the external form of the larvae. That of *S. vivipara* has retained its elliptical shape and shows no trace of ciliated bands, while the other has assumed the familiar auricularia form. Furthermore, there is no trace of calcareous structures of any kind in *S. vivipara* to correspond with the plates at the posterior end of auricularia. In the latter also, Semon ('88) has figured and described a larval nervous system, but after careful investigation of this point, I am convinced there is none in the larva of *S. vivipara*. In external form, the latter is very regular, but with the growth of the coelomic pouches the ectoderm of the dorsal surface begins to become thinner and more flattened, while that around the mouth, especially posterior to it, shows a tendency to increase in thickness. This difference between the dorsal and ventral surfaces may sometimes be seen in very young larvae and is clearly shown in figure 22. Before the two coelomic vesicles have entirely separated, the hydrocoel has become considerably larger and begins to grow anteriorly and toward the right, while about the same time five outgrowths begin to appear on that side which is furthest from the fore-gut (Fig. 15). Soon after their appearance *five* other much smaller outgrowths arise, one at the right of each of the first five. The first series gives rise to the five primary tentacles, and the second series corresponds to those which in *S. digitata* give rise to the radial water-canals. In *S. digitata* however, there is a sixth outgrowth at the extreme left, the rudiment of the Polian vesicle, but in *S. vivipara* this vesicle is not formed until after the closure of the hydrocoel ring. The water-canal enters this ring at a point just between the fourth primary tentacle (counting from before backwards) and the fourth secondary outgrowth (Fig. 23). In this particular my observations confirm Bury ('89) in opposition to the statements of Semon ('88).

Before the outgrowths of the hydrocoel are very evident, that part of it which lies dorsally and in immediate connection with the water-canal bulges out, becomes thinner-walled than the rest of the hydrocoel, and gradually separates from it, but before the separation becomes marked, the outgrowth diminishes in size and with the increasing growth of the water-canal disappears. This structure, I believe, is the "anterior coelom" which Bury ('95) has shown to exist in the auricularia of *S. digitata*. It is very marked in some specimens of *S. vivipara* (Fig. 24), and I see no reason to doubt Bury's interpretation. He does not make very clear what the ultimate fate of this coelom is in *S. digitata*, but leaves the impression that it is connected with the subsequent formation of the madrepore plate, as Ludwig ('91) considers it to be in Cucumaria. In *S. vivipara* however, there is seldom any trace of it left after the hydrocoel ring closes, and there is no reason to suppose that it has any connection with the much later madrepore openings. About the time of the appearance of the primary tentacles, the larval anus, which was the original blastopore, closes entirely and the digestive tract ends blindly. Accordingly we now have a regular elliptical larva, about a third of a millimeter long, with the ventral ectoderm much thicker than the dorsal, without ciliated bands, calcareous particles, or nervous system, a mouth on the anterior ventral surface but no anus, a well-developed coelomic pouch on each side of the digestive tract, and a hydrocoel with five primary tentacles and five secondary outgrowths, opening to the exterior through the dorsal pore, by means of an *adradial* water-canal, upon which may still be seen the vestige of an anterior coelom.

6. THE DEVELOPMENT OF THE PENTACTULA.

In such larvae, the ectoderm of the ventral surface continues to thicken and before long is sharply set off from the ectoderm of the rest of the body, which consists of a single layer of cells. The thickened ectoderm forms a circular field around the mouth though the latter does not lie at its center, but nearer to its anterior edge. This circular disc gradually sinks below the level of the rest of the ectoderm, and the latter grows in over it from all sides, until the disc lies at the bottom of a shallow cavity, the so-called "atrium," which opens on the ventral surface through a small pore (Fig. 16). This pore does not lie directly over the mouth, but either before or behind or somewhat to one side. While these external changes are taking place, the hydrocoel has continued its growth, the anterior end passing across on to the right side of the larva where it bends downward and backward around the oesophagus to meet the posterior end near the middle line. The primary tentacles have increased considerably in size and are growing up around the floor of the atrium, while the secondary outgrowths also grow *upward* beside them. No Polian vesicle has yet appeared, and no marked distinctions between the different parts of the digestive tract are to be seen, but the latter has become very much arched toward the dorsal surface, and the lumen of the middle section is larger than at either end. A new anus may have been formed by the end of the hind-gut growing to the body-wall on the ventral side and an opening breaking through, but in some cases the definitive anus does not appear until the pentactula form is nearly attained. The most important changes have been going on meanwhile in the coelomic pouches, the growth of which has been very rapid. The left vesicle has grown more anteriorly than the right, and sends forward two finger-like processes, one of which passes across the median line into the right side of the larva, while the other grows up to the inner side of the hydrocoel ring, above the most posterior tentacle, and follows the course of that ring around the oesophagus (Figs. 26–28). These anterior prolongations of the left coelom were observed by Bury ('89 and '95) in *S. digitata*, but have apparently been overlooked by other investigators. The one which passes on to the right side of the body fuses so soon with the right coelom that I have been unable to confirm Bury's further observations regarding it, and in *S. vivipara* its appearance might easily be entirely overlooked. But the prolongation which passes to the hydrocoel remains distinct through all the later stages of the larva, and its subsequent changes are easy to trace. It soon loses its connection with the left coelom and forms a tube, lying on the oral surface of the hydrocoel ring. Meanwhile the right and left coelomic pouches have met and fused on the ventral side of the digestive tract, while dorsally they are still separate, the right pouch extending considerably further back than the left. The larva has now reached the condition shown in Fig. 16. In its subsequent growth the atrium, with its thick ectodermal floor and narrow opening to the exterior, moves to the anterior end of the larva, where it finally comes to lie, along with the mouth, oesophagus, and hydrocoel ring. The latter has now closed, without the formation of a Polian vesicle, somewhat to the left of the middle line apparently (Fig. 25), but I am not sure that the point of closure is always on the left side, for it is by no means easy to determine the exact mid-line. With the closure of the hydrocoel, occurs the union of the two ends of that coelomic tube which lies on its oral surface, so that we now have a circular sinus around the oesophagus just above the water-ring. This sinus is very evident in young Synaptas, and Bury's ('95) surmise regarding its origin from the left coelom is entirely correct. The primary tentacles are growing upward, not pushing the floor of the atrium out before them, as Semon ('88) says, but enclosing the atrium within their circle so that the thickened sensory epithelium, which they subsequently possess, does not arise as Semon describes. It is clear, from Figs. 16 and 17, that his description could not possibly apply to *S. vivipara.* The secondary outgrowths remain nearly unchanged in size and show no sign of bending backward to form radial canals. The Polian vessel is formed as an outgrowth on the inner side of the hydrocoel ring in the *left dorsal* interradius, as Ludwig ('23) found it to be in Cucumaria.

The digestive tract grows with greater rapidity relatively than any of the other organs. Accordingly, the oesophagus pushes upward toward the atrial opening, so that the thickened ectodermal floor of the atrium lies surrounding it, in the form of a poorly defined circumoral ring. Continued growth pushes the oesophagus against the upper ectodermal wall of the atrium, and with that it fuses, leaving the circumoral ring entirely cut off from the outer ectoderm of the body (Figs. 87 and 88). Meanwhile the growth of the primary tentacles has pushed this body-wall upward and outward, so that the narrow slit-like opening of the atrium is gradually widened until it finally disappears, leaving the ectodermal-covered, anterior end of the oesophagus to form the definitive mouth, in the center of the circle of tentacles. This process is not completed however, until the pentactula form is fully assumed. The differences between this development of the mouth and circumoral ring and that given by Semon ('88) for *S. digitata* are almost irreconcilable, but they are all dependent on the question, whether the five primary tentacles push up through the floor of the atrium or grow up around it. The latter is certainly the case in *S. vivipara.* While these changes are taking place anteriorly, the hind-gut has increased in length so that it has not only arched still more toward the dorsal surface but has bent on itself and formed a loop lying to the left of the stomach. The coelomic pouches already united and forming a single cavity ventrally, have met in, or close to, the mid-dorsal line and by the union of their walls have formed the dorsal mesentery. This mesentery follows pretty closely the curve of the intestine and attaches it throughout its course, to the body-wall. The water-canal lies in the anterior part of the mesentery, but whether that part was formed in a different manner, as Bury ('95) thinks probable, it is impossible to say from observations on *S. vivipara.*

Meantime most important changes are going on in the circumoral ring of ectoderm which we have seen was formed from the floor of the atrium. This ring is the beginning of the central nervous system, and from it the tentacle and radial nerves arise. As the primary tentacles push upward past the atrium, they lie closely appressed to its floor and wall. They retain this position even after the circumoral ring is pretty clearly defined, and before they have grown much above it, the radial nerves appear between each pair of them as outgrowths of the central ring. These outgrowths pass directly over the secondary outgrowths of the water-vascular system and bend backwards to run toward the aboral pole of the body. Very soon after they appear (not before them, as Semon ('88) describes for *S. digitata*), that part of the circumoral ring appressed to each primary tentacle begins to grow upward with it on its inner side, forming the tentacle nerves. As the tentacles continue to grow and press the anterior body wall outward, the ectoderm which covers them at the tip becomes noticeably thickened, especially on the outer side (Fig. 54), and apparently assumes a sensory function, probably in connection with the tentacle nerve. The formation of the otocysts of Thomson ('62), the "hörorgane" of Baur ('64), takes place as described by Semon ('88). They arise by evaginations from the outer side of the circumoral ring close beside the outgrowths which form the radial nerves. With the growth of the latter, the otocysts come to lie external to them at the point where they bend backward, and in this position the sense-organs remain throughout life. It is a very evident and noteworthy fact that the development of the radial nerves and otocysts does not take place at the same time in the five radii, but there is a marked difference between them. The first to appear is that nerve which subsequently indicates the mid-ventral radius, and with it appear its two otocysts. The two lateral ventral nerves appear next, and with them the otocyst which accompanies each one on its ventral side. The lateral dorsal nerves next appear (Fig. 1), and very soon afterwards the two other otocysts of the right and left ventral radii are formed. Last of all to develop are the otocysts of the right and left dorsal radii. This sequence in the appearance of these nerves and sense-organs is probably connected with the fact already mentioned, that the thickened ectoderm which made up the floor of the atrium did not lie symmetrically around the mouth, but the greater part of it was posterior or, when the mouth lies at the anterior end of the larva, ventral to it. What the significance of this condition may be, I am unable to suggest, but it is interesting to note that in Cucumaria Ludwig ('91) found the ventral radius the most advanced in development. Any possible similarity ends here however, for the development of the other radii was quite the reverse in Cucumaria of what it is in Synapta.

About the time of the completion of the pentactula form, there appear in the ectoderm of various parts of the body peculiar invaginations (Fig. 41) which are finally connected with the exterior only by a very narrow canal (Figs. 12 and 13, and Fig. 17, lgo.). These organs appear, from their structure and the great variation which they show in staining, to be of a glandular nature, and I am inclined to think they may be connected with the absorption of nourishment from the fluid of the body-cavity of the mother, for they never increase in size, are most abundant in the young with ten tentacles, and seem to have entirely disappeared in the adult, and finally, nothing of the kind has been described for any other holothurian. When fully grown they measure about fifty mikrons in diameter and somewhat less in depth. They consist of very long, clear cells, with nuclei at the extreme distal ends, surrounding a more or less spacious lumen which opens to the exterior by a narrow canal of ordinary epithelial cells. Sometimes the clear cells stained heavily, but often they did not stain at all.

Up to this time the mesenchyme cells have played no part in the development of the larva. In Fig. 16, they are shown as they appear scattered almost uniformly through the segmentation cavity. Shortly after this, however, they begin to gather around the lower and outer edge of the water-vascular ring, and by the time the pentactula stage is reached they have begun the formation of the calcareous ring. Contrary to Semon's ('88) views on *S. digitata*, and in accordance with Ludwig's ('91) observations on Cucumaria, I have found no evidence at all of any mesenchymatous musculature on the oesophagus. The first products of the mesenchyme cells to appear are five small straight rods between the primary tentacles but outside and somewhat below the hydrocoel ring. Soon after these, five more appear below the bases of the tentacles, so that there are now ten rods, five radial and five interradial, and they continue in this position so long as there are only five tentacles. I saw no evidence at all of any such shifting of position of the first five rods as Semon ('88) records for *S. digitata*, nor could I consider the position of the second series as agreeing at all with his description. Very soon after the appearance of the ten rods, they fork at the ends and begin to branch very irregularly. As will be seen from Fig. 46 a–i, the divisions occur at all sorts of angles and not only differ decidedly from Semon's figures of the same rods in *S. digitata* but show no sign at all of following his law ('87) for the formation of calcareous plates in Echinoderms. The much-branched ends of the rods come into very close contact but evidently never mingle, for the plates into which they develop are at all times easily separable and the line of division between them is practically straight. Very soon after the appearance of the first five calcareous rods, the radial nerves grow backward over them and before the completion of the pentactula, run to the posterior end of the animal.

We have now reached the complete pentactula form, a slightly older stage of which appears in Fig. 18. The pentactula is about half a millimeter long and its characteristics may be briefly summed up as follows: — Water-vascular system consisting of a closed hydrocoel ring or circumoral water-tube with five primary tentacles, between which are five very much smaller but equally erect secondary outgrowths; a water-tube in the mid-dorsal interradius connecting the circumoral ring with the exterior; and a Polian vessel in the left dorsal interradius. Nervous system consisting of a circumoral ring; five tentacle nerves on the inner face of the primary tentacles, the ectoderm of which is considerably thickened, especially on the outer side; five radial nerves bending backward over the secondary outgrowths of the water-ring and over the radial pieces of the calcareous ring, and running to the posterior end of the body; and five pairs of otocysts, lying external to the radial nerves, where they bend backward. Digestive system, consisting of a short oesophagus with the mouth opening anteriorly in the center of the circle of tentacles, a large stomach, a comparatively short intestine with a single loop in it, and usually an anus formed secondarily near or at the aboral pole. Digestive system attached to the wall throughout its whole course by a mesentery, formed by the union of the two walls of the right and left coelomic pouches. Calcareous ring consisting of five radial and five interradial pieces with much-branched ends. A few scattered glandular organs of doubtful function in various parts of the ectoderm.

7. The Development of the Adult Synapta.

Since there is no cessation of growth nor any resting period on the assumption of the pentactula form, it is impossible to draw any hard and fast lines which will always serve to distinguish that stage. For many larvae, which appear to have only five tentacles, show on careful examination the rudiments of new ones, and other larvae which show no tentacles externally show the perfect pentactula form, when sectioned. As soon as the five primary tentacles have pushed out so far as to entirely obliterate the original opening of the atrium, the secondary outgrowths of the water-ring, which have hitherto scarcely shown any indication of growth, begin to develop and push upward. As we have already seen, the radial nerves lie directly over them, so that they cannot grow straight up but push out to one side or the other of the nerve. The outgrowth which lies in the mid-ventral radius, however, develops very slightly and does not normally push out on either side of the nerve which overlies it. The outgrowths which lie in the right and left ventral radii take the opposite course, and broadening out laterally, grow up on both sides of the nerves which overlie them, to form accessory tentacles. The outgrowth of the right dorsal radius pushes out on the dorsal side of its overlying nerve and forms an accessory tentacle in the mid-dorsal interradius, while the outgrowth of the left dorsal radius shows as yet little tendency to develop either way (Fig. 35). Consequently we now have a larval form with ten tentacles, two in each interradius. As the accessory tentacles grow very rapidly they are soon equal in size to, and cannot be distinguished from, the five primary tentacles. It is hard to decide positively which of the five accessory tentacles develops first, for apparently they all begin to grow at about the same time. In *Chirodota rotifera*, Ludwig ('81) found the first two accessory tentacles in the lateral dorsal interradii, and he does not speak of finding any trace of additional tentacles in the other interradii. I have not found any stage similar to that in *S. vivipara*, and I think the five accessory tentacles appear at practically the same time. It is an important and interesting fact, however, that the five accessory tentacles are formed in precisely the same manner and from the same radii as the *second* series of five tentacles in Cucumaria, (Ludwig, '91). It seems to me that this fact proves satisfactorily that the radial canals in Synaptidae are homologous with those of the other holothurians or, more accurately, the secondary outgrowths of the hydrocoel ring in the Synaptidae are homologous with the five outgrowths of the hydrocoel ring in the true holothurians. In both cases, the ten-tentacled young has one primary and one accessory tentacle in each interradius. While this change is taking place in the number and arrangement of the tentacles, a corresponding change is going on in the calcareous ring. As the accessory tentacles push out into the interradii, the calcareous rod which lies at the base of the primary tentacle comes to lie between it and the accessory tentacle. I could not see that this came about by any actual movement of the rod itself, but was due simply to the increase of width in each interradius. In the further growth of the calcareous ring, the interradial pieces send up projections between the two tentacles (Fig. 46 h) and at the same time branch and divide so rapidly and irregularly that they soon become plates, with straight sides but pointed anteriorly and notched behind, made up of a very fine irregular network of calcareous strands (Fig. 44). The radial plates develop in the same way but send up two projections, one on each side of the radial nerve (Fig. 46 i), which finally fuse together above it and thus form the perforated plates of the ring (Fig. 45). About the same time, the mesenchyme cells lying between the ectoderm and the wall of the coelom begin to gather in groups close to the ectoderm and there give rise to anchors and anchor-plates so characteristic of the adult Synapta. The development of the calcareous bodies from a straight rod takes place as described by Semon ('87) for *Synapta inhaerans*. While these deposits appear in the body-wall as far anteriorly as the base of the tentacles, in the walls of the latter, lying parallel to the long axis, there appear numerous rather long, more or less, knobbed rods (Fig. 48) similiar to those described by Semon ('87) from the tentacles of various synaptids. These become very abundant in the older ten-tentacled larvae.

The digestive tract meantime has increased in length, and the stomach is more clearly marked off from the intestine and oesophagus. The nervous system has not undergone any marked changes, but each of the accessory tentacles is supplied with a nerve on its inner side, as in the case of the primary tentacles. In various parts of the skin, especially anteriorly, clusters of ectoderm cells are to be found which later form the so-called sense-papillae ("Tastpapillen" of Hamann, '83). I have been unable to find any connection between these spots and the nerves until a very much later period, and I cannot decide how or when this connection is made. The glandular organs previously described are very abundant at this stage, especially posteriorly. Soon after the pentactula form is complete, the walls of the coelom and of the hydrocoel begin the formation of muscle fibers, always on the side turned from the cavity which they enclose. The first to appear are the longitudinal muscles of the tentacles and radii. The former appear as fibers on the outside of the tentacle canals and they soon form quite a thick layer. The radial muscles arise within a fold of the coelomic wall, which appears along the inner side of the radial nerves. This fold begins anteriorly near the calcareous ring and runs backwards with the nerve, enclosing a considerable space between its walls. In this space the muscle fibers arise from the endodermal cells of the coelom. Later on, the circular muscles of the body appear, arising from the outer side of the coelomic wall also. They cross the space in which the longitudinal muscles lie, forming a layer between the latter and the nerve. At the same time, the longitudinal and circular muscles of the digestive tract, and the muscles of the water-ring, begin to appear, so that by the time the ten-tentacled stage is reached, the musculature is practically that of the adult. With the appearance of the longitudinal muscles of the tentacles, comes the development of the valves at the openings of the tentacular canals, close to the upper edge of the calcareous ring.

Before the accessory tentacles have begun to appear, there arises on the right hand side of the mesentery which fastens the intestine to the wall of the left interradius a longitudinal fold or evagination of the epithelium close to the intestine (Fig. 58). This fold follows the course of the intestine, with the mesentery on the dorsal side and grows forward along the stomach and backward toward the anus. Later a similar fold appears in the coelomic epithelium on the opposite (ventral) side of the digestive tract and the two folds soon become connected around the intestine and stomach by numerous ill-defined lacunae between the coelomic wall and that of the digestive organ itself. These vessels are the first stages of the blood vascular system and into them cells from the coelomic epithelium pass to form the blood corpuscles. Theoretically the vessels ought to be lined with connective tissue of mesenchyme cells but these are so few in the early stages of the larva, that the connective tissue between the laminae of the mesenteries or even around the digestive tract is very hard to demonstrate. The main blood vessels appear to be purely entodermal in origin and their walls seem to be made up solely of the coelomic wall. At any rate, the dorsal vessel does not arise in *S. vivipara* in the way given by Semon ('88) for its origin in *S. digitata*, by a simple split in the mesenchyme where the two coelomic folds unite above the intestine to form the mesentery.

Very soon after the pentactula stage is reached the first rudiment of the genital system appears. It arises on the inner side of the right-hand lamina of the dorsal mesentery between the stone-canal and the oesophagus. The first appearance is simply the increased size of the cells at this point, resulting in a thickening of the wall (Fig. 32), but the cells soon multiply rapidly and form a more or less spherical mass within the mesentery (Fig. 33). As this mass increases in size, cavities appear within it (Fig. 34) and these increase in size and begin to unite together until they form one central lumen for the gland (Fig. 35). Meanwhile the right lamina of the mesentery forms an outer epithelium which soon becomes quite distinct from the central mass of cells. Between this epithelium and the remainder of the gland a few mesenchyme cells form an extremely scanty connective-tissue layer. In the full-grown ten-tentaculed larva, the genital gland is plainly seen (Fig. 19), lying entirely on the right-hand side of the mesentery, near the stone-canal.

The ten-tentacled larva (Fig. 19) is a more clearly defined stage in the development of *Synapta vivipara* than is the pentacula; that is, it seems to last longer, and the relative condition of development of the various organs is more constant. The changes which occur subsequently in the assumption of the adult form must now be considered. The most obvious of these is the increase in the number of tentacles which arises from the addition of another tentacle to the right and left dorsal interradii (Fig. 86). The extra tentacle of the left side arises from the left dorsal "secondary outgrowth" of the hydrocoel ring, which has hitherto remained in its original position beneath the left dorsal nerve but now pushes out on its lower or ventral side and forms the eleventh tentacle. At the same time, the extra tentacle of the right side arises from the lower or ventral side of the right dorsal "secondary outgrowth" which pushes out on that side of the right dorsal nerve and forms the twelfth tentacle. Not infrequently individuals are found with thirteen tentacles, and in these the extra tentacle is usually in one of the ventral interradii. In such cases it is probable that the mid-ventral "secondary outgrowth" has grown up on one side or the other of the mid-ventral nerve, although in normal specimens it does not develop at all. Occasionally the extra tentacle is in the mid-dorsal interradius, and in such cases it is probable that the left dorsal "secondary outgrowth," which normally develops only a single tentacle, has given rise to a second on the dorsal side of the left dorsal nerve. Corresponding to these changes in the number of tentacles additional plates appear in the calcareous ring, but these plates do not arise by interpolation of new rods. On the contrary, the plate of the same radius with the new tentacle increases its length and sends upward a new projection for the support of the tentacle (Fig. 47), and this subsequently forms the center of the new accessory plate. In specimens of the calcareous rings cleaned with caustic soda, it seemed to me that the calcareous plates of the right and left dorsal radii were less easily separated from those plates on their ventral side than from those on the dorsal, so I am inclined to think that for a time, if not throughout life, these two plates remain in closer union than any of the others. In specimens with thirteen tentacles, there is an additional plate in the calcareous ring corresponding to the extra tentacle. About this same time the miliary granules (Fig. 50) begin to appear in various parts of the body-wall and in the tentacles. Like all other calcareous concretions of Synapta, they are formed by mesenchyme cells. They usually appear in clusters of several hundred, which continue to increase in number afterwards until it may reach thousands. By the time twelve tentacles have appeared, the genital gland begins to push over on the left hand side, but it is not until long after the adult form is assumed in all other respects that the left branch of the gland equals the right in size. As soon as the left branch is well started, the germinal epithelium begins to push upward in the mesentery beside the stone-canal, and forms the genital duct, but does not reach the outer body-wall for some time. This account of the development of the genital duct accords with Mortensen's ('94) observations on *Cucumaria glacialis*, although his account of the origin of the genital gland itself differs considerably from my observations. Important changes are going on meanwhile in the nervous system. From the inner side of the circumoral ring nerves or bands of nervous tissue arise and pass inward to the oesophagus. These will be referred to more fully in describing the nervous system of the adult. Even in the ten-tentacled stage, before the remaining two tentacles have made a fair start, there arises on each side of the tentacle nerve at its base a knob-like outgrowth which becomes covered over with a peculiar mesenchyme layer, and these form the "eyes," which also appear at the base of the eleventh and twelfth tentacles, after they receive their nerves from the circumoral ring. With the appearance of these eyes, the first trace of pigment appears in the mesenchyme not only about them but in various parts of the body, especially around the calcareous ring. This pigment on its first appearance is bright green, even about the eyes, so that at this stage the eyes of the young Synapta are very conspicuous as large green spots at the base of the tentacles. Very soon, however, a dark reddish brown pigment appears, but this is probably an older stage of the green, and not a different pigment; for the pigment around the eyes soon loses its green color and turns brown, and there is no reason to assume that the pigment in other parts of the body is any different from that around the eyes. All of the pigment arises in the connective tissue, and is apparently a product of the mesenchyme cells. It is especially abundant at the anterior end of the body, and above all other places in and around the calcareous ring.

Before the number of tentacles is complete the ciliated funnels so characteristic of Synapta begin to appear on the mesentery, near the body-wall. These funnels arise from a large cell or group of cells in the endodermal epithelium of the mesentery (Figs. 61 and 62a). The multiplication of these cells soon forms a hemispherical outgrowth (Fig. 62d) which increases in size and becomes more and more spherical in shape, until it is finally attached to the mesentery by only a narrow stalk (Fig. 62e). It then begins to flatten on one side, and the cells of its outer layers become smaller and stain more heavily than those nearer the stalk (Fig. 62f). The flattened surface at last becomes concave and the funnel shape begins to be assumed. At the same time, the stalk becomes elongated and draws up within it some of the connective-tissue layer of the mesentery, which becomes the supporting layer of the funnel. Even during the ten-tentacled stage the digits of the tentacles begin to be formed, but they do not become prominent until the twelve tentacles are all developed. The digits arise as evaginations of the water-canal of the tentacle (Fig. 56) which very soon become shut off from the main canal and in the adult have no connection with it (Fig. 55). The earliest ones to appear are near the middle of the tentacle, and the later ones appear both proximally and distally to them. The digits form longitudinal muscles on the outer side of the central cavity in the same way as the tentacles themselves. They are also supplied with nerves from the main tentacle nerve. The peculiar glandular organs of the larva are no longer forming but seem rather to be disappearing, and the longitudinal rods of the tentacles reach their maximum number at this time. The circumoral sinus, which was entirely cut off from the rest of the coelom in the pentactula stage, has increased greatly in size (Fig. 89) but is now in open communication with the body-cavity, though strands of connective tissue traverse it, uniting the oesophagus to the water-ring and, higher up, to the coelomic wall. With the greatly increased size of the young Synapta, comes a considerable change in the relative position of the organs in the body-cavity. The body has grown much posteriorly, drawing out with it that part of the intestine which lies in the right ventral interradius. The nerve ring is drawn upward with the growth of the tentacles, so that it comes to lie very near the ectoderm at their base. The increased length of the tentacular canals has pushed the water-ring downward so that it lies some distance below the calcareous ring (Figs. 90 and 91), but it is still in open communication with the exterior by means of the water-canal (Fig. 66). Mesenchyme cells have formed a few calcareous rods about the latter (Fig. 49), especially near the point where it passes into the body-wall. Just within the body-cavity from this point, openings have appeared on it which place its interior in direct communication with the body-cavity, so that the water-vascular system combines the primitive external opening of the pentactula with the internal madreporitic openings of the other holothurians. The mesenchyme cells around the calcareous ring have formed on its posterior edge a connective-tissue ring, which later becomes so prominent in the adult as the cartilaginous ring.

In concluding this account of the embryology it may be well to summarize briefly the derivation of the different organs from the germ layers of the gastrula.

Ectoderm. From the gastrula-ectoderm arise the ectoderm of the adult, the sensory epithelium of the tentacles, the entire nervous system including all the sense organs, the larval glandular organs, and a small part of the oesophagus. Possibly the extreme posterior part of the rectum is also ectodermal.

Endoderm. From the gastrula-endoderm arise first of all the scattered mesenchyme cells which make up the mesoderm. Soon afterwards the hydroenterocoel is divided off. The remainder of the archenteron forms simply the lining of the digestive tract, including most of the oesophagus. From the hydroenterocoel, the coelomic pouches are constricted off, leaving behind the hydrocoel, from which the entire water-vascular system, and also the cavities of the digits, arise. The longitudinal muscles of the tentacles and digits come from the epithelium of the hydrocoel. The coelomic pouches form the peritoneal lining of the body-cavity and the epithelial covering for the various organs contained in it. All the muscles of the body-wall, gut, genital glands, water-ring, and Polian vessels are also derivatives of the endoderm. The genital organ, including the genital duct, and the ciliated funnels are likewise derived from the wall of the coelom. The haemal system is also covered by the epithelium of the coelom and apparently arises as evaginations of the same, while the blood-corpuscles certainly come from that layer.

Mesoderm. From the mesenchyme cells, arising from the archenteron of the gastrula, come all the connective tissue of the body, the pigment, the covering of the eyes, all the calcareous concretions (including the calcareous ring), and the cartilaginous ring. No trace of mesenchymatous musculature was found anywhere, and the part which the mesoderm takes in the formation of the haemal system is certainly inconsiderable.

8. The Anatomy of the Adult.

Although the anatomy of the European Synaptas is so well known, thanks to the investigations of Baur ('64), Semon ('87), Hamann ('83 and '89), Cuénot ('91), and others, there are so many points in which *Synapta vivipara* differs from the forms hitherto examined, it seems desirable to add a few words concerning these and other points. Except in the case of sense-organs, no attempt has been made to go into the histology, but my attention has been confined to the more general features of the minute anatomy. In the structure of the body-wall and the muscular system, there are no important features to mention, aside from the shape of the longitudinal radial muscle bands. Each of these bands is forked at its anterior extremity, and the two branches are attached to the radial calcareous plate, one on each side of the radial nerve. These branches soon unite as they pass backward, and form a single narrow band, which extends far out into the body-cavity. But still further back, it decreases in depth and increases correspondingly in width, and the epithelium which covers it tends to fuse at the outer edges with the epithelium of the body-cavity, so that at numerous points in its course the muscle has acquired secondary attachments to the body-wall. During the greater part of its course, it is a nearly flat band, but as it approaches the extreme posterior region of the body, it tends to become cylindrical, and where it ends near the anus the cross-section is circular. These changes in shape will be made clear from Figs. 94–100. The structure of the genital glands has already been given in detail, and the openings in the wall of the rectum have also been sufficiently described. The blood-vascular or haemal system is very simple, consisting of a dorsal and ventral vessel on the intestine and stomach with connecting lacunae in their walls. Posteriorly, both vessels end about half way down that section of the intestine which lies in the right ventral interradius (Fig. 92). Anteriorly, the ventral vessel ends a little in front of the stomach, on the oesophagus. The dorsal vessel runs forward to the water-ring and forms on its inner side a circumoesophageal ring, from which branches pass on to each tentacular vessel. The dorsal blood-vessel also seems to open out in the mesentery to form broad lacunae about the genital gland, such as Cuénot ('91) found in European Synaptas, but I never found coagulated blood there as in the dorsal vessel, and I do not feel sure that such lacunae actually exist. The ventral vessel of the stomach does not lie appressed to its wall, but entirely free from it and connected with it by several small branches. It is also connected by a large transverse vessel with the ventral vessel of the intestine (Fig. 92), and the two sections of the latter are also connected by a similar vessel. These transverse vessels do not appear until the animal is several centimeters long, when they arise by outgrowths of the coelomic epithelium of stomach and intestine which, lying close together as they do in the loops of the digestive tract, touch and fuse (Figs. 59 and 60) and with the increased growth of the intestine are finally drawn out to slender connecting vessels. Like the vessels of the young Synapta, these are supposed to be lined with connective tissue, but I have been unable to detect it in their walls.

The ciliated funnels of *Synapta vivipara* differ considerably in appearance from those of *S. digitata* or *S. inhaerans*, though they do not differ essentially in structure. Only one sort seems to be present and these are quite small but extremely numerous on all three of the mesenteries. They measure from 40μ to 75μ in length, and from 30μ to 40μ in breadth and depth, which is only about half the size of those of *S. digitata*. They are broad funnel- or cornucopia-shaped in outline and usually have a short stalk. Their general structure will be easily understood from Figs. 63–65. The water-vascular system consists of a circumoesophageal ring from which canals arise and pass to the tentacles, into which their entrance is guarded by well-developed valves. Each tentacle rests on the calcareous ring in such a way that the outer half of the base is on the outside of the calcareous plate, forming a sort of rudimentary ampulla (Fig. 90). There is not in the adult, any more than in any of the larval stages, the slightest trace of radia. water-canals. Dependent from the ring-canal there is always present in the left dorsal interradius a slender Polian vessel five or six millimeters long, and in nearly all adults additional Polian vessels, sometimes as many as six, are present in the ventral interradii. The stone-canal leaves the water-ring on the left-hand side of the mid-dorsal interradius and does not lie in the dorsal mesentery but clearly separate from, and to the left of it. It soon passes into it, however, on its outward course and runs to the body-wall close beside the genital duct (Figs. 66 and 67). It enters the body-wall on the right of the mesentery and bends upward more or less abruptly, opening finally to the exterior close behind the circle of tentacles (Figs. 66–70). In exceptional cases there are two openings (Figs. 71–73) or rarely the reverse happens and the canal closes before the exterior is reached. Besides this external opening, the stone-canal also opens into the body-cavity through a well-developed madrepore (Figs. 66 and 74). Throughout its course the canal is heavily ciliated, and especially so around these madreporitic openings, the whole arrangement being admirably adapted for keeping the body-cavity fluid well aerated.

The nervous system consists as in all Synaptidae of the central circumoral ring with the five radial branches and the smaller branches to each of the tentacles, but there are some additional nerves and certain of the sense-organs which have not been figured hitherto. Each of the radial nerves is divided longitudinally into an outer and an inner band as in other Synaptas, but, unlike them, there are no canals or vessels of any kind accompanying the nerves. There are, therefore, in the radii of *S. vivipara*, no spaces or lacunae in connection with either the blood, water, or nervous systems, but they are marked simply by the longitudinal muscles and nerves (Fig. 99). Each tentacle-nerve sends off branches to the digits (Fig. 55), so that almost the whole surface of the tentacle becomes sensory. On the base of the tentacles and in various parts of the ectoderm all over the body, there are numerous sense-buds or "taste-papillae," (Fig. 84), such as were first described by Hamann ('83). The structure of these organs has been well described by him and still more recently by Cuénot ('91). My observations support the opinion of the latter, that under each one of these sense papillae there lies a small ganglion. From the lower side of the circumoral ring, there arises between every two tentacles a broad band-like nerve (Figs. 75 and 76) which runs inwards towards the mouth, innervating the ectoderm of the oral disc as well as the muscles of the oesophagus. Hamann ('83) describes a single nerve to the oesophagus, and Semon ('88) speaks of it in *S. digitata*, but so far as I can learn no other nerves from the inner side of the ring have been described in holothurians. At the base of each tentacle, there are easily seen a pair of reddish brown spots, the so-called eyes (Figs. 77 and 78). Similar spots are mentioned in various Synaptas by Müller ('50), Baur ('64), and Semper ('68), but Semon ('87) and Hamann ('84) seem to doubt their visual function. There can be little doubt, however, that in *Synapta vivipara* these eyes are actually of service as light-detecting organs. In position and general structure they resemble those described by Ludwig and Barthels ('91) for *Synapta vittata*. They consist of a distinct, rather horny mesodermal layer, of a light brown color, containing scattered nuclei, overlying the swollen end of a large nerve which arises on each side from the base of the tentacle-nerve (Fig. 77). The ends of these nerves are made up of large nerve-cells with large nuclei, which are somewhat swollen and apparently vacuolated at their outer extremities. They are polygonal in outline, when seen in cross-section (Fig. 79), and the inner ends taper off into fibers which run out into the nerve (Fig. 80). The mesodermal covering, which also has the appearance of being vacuolated, is clearly a continuation of the thin mesoderm layer which surrounds all the nerves. The eyes are about 60μ in diameter, the mesodermal covering being six or eight mikrons thick. That this covering may be affected by light is probable, for its color is due to the pigment it contains. The other noteworthy sense-organs are the otocysts

(Figs. 81–83), already mentioned as lying external to the radial nerves at the point where they bend backwards over the calcareous ring. They are much smaller than those figured by Cuénot ('91) for *S. inhaerans* and differ from them in having only a single large vesiculated cell enclosed within them, instead of a number of small ones. The otocysts of *S. vivipara* measure only about 60–70μ in diameter, while the contained cell is almost a quarter as large. In no case have I found more than one cell enclosed in an otocyst of this species. Hamann ('84) suspected that they were larval organs having no function in the adult, but Semon ('87) has already proved that idea erroneous, as Hamann ('89, p. 308) has since admitted. If any further evidence were needed, it could be found in the increase of size of the organs during the development of the animal (Figs. 81–83) as well as in the very obvious connection with the radial nerves. But I am inclined to the view that these so-called otocysts do not function as hearing organs at all, but are of use to indicate the animal's position. Semon ('87) was unable to find any cilia in them, and his experiments on living Synaptas brought him to the conclusion that they were deaf to sound waves. If the enclosed cell is vesiculated, as it appears to be, it must float in the fluid with which the otocyst is filled and so presses on that part of the wall which is uppermost. Any change in the position of the animal would cause a corresponding change in the position of the enclosed cell and thus give rise to a changed sensation.

The fully grown *Synapta vivipara* (Fig. 20) measures from ten to fifteen centimeters in length and from four to nine millimeters in thickness; the size depending largely on the state of contraction of the muscles. In color they vary from a pale reddish brown to a very dark greenish brown more or less spotted and blotched with white. The ground color is due to the pigment in the connective tissue of the body-wall and varies greatly with the amount of that pigment, but the white spots and blotches are due to the aggregation of great numbers of the miliary granules, just beneath the ectoderm. The pigment is not affected to any extent by pure alcohol, but corrosive sublimate and all acids destroy or greatly modify it. Just posterior to the calcareous ring and in connection with it there is a ring of cartilage-like connective tissue (Fig. 90). This structure was described and figured by Théel ('86), who also figured the anchors and plates from the body-wall, in his account of *S. picta*. The anchors (Fig. 51) lie close under the ectoderm and parallel with it, at right angles to the main axis of the body. Each anchor is much curved or bowed inwards, while its arms or flukes are curved outward so that the points of the arms are always projecting. The vertex is not toothed but has five or six almost spherical knobs on its edge. The posterior end is broadened out into several short, very finely-toothed branches. Beneath the anchors lie the rounded, smooth-edged, somewhat arched plates, which normally possess seven large toothed holes

(Fig. 52) and two large and three small smooth holes. On the side of the plate next to the anchor and near the posterior end is an arched bow, which bears a few teeth on its anterior edge. Increased growth of the plate often increases the number of holes (Fig. 53), but as a rule they are very constant. The calcareous rods which were so abundant in the tentacles of the young larvae are so few that for a long time I was led to consider them entirely wanting. The tentacles (Fig. 57) of the adults are long and slender with from 12 to 18 pairs of digits, but the number varies greatly with the age and size of the animal. The glandular organs which characterize the young ten-tentacled stage seem to be entirely wanting now; at any rate, I have never found any trace of them in an adult.

A number of interesting monstrosities were found, chiefly among the older embryos. One of these is shown in Fig. 93, but some of the others were much more complicated, consisting of three, four, and, in one case, five young, which had grown together, or budded from each other in various ways. Among adults, besides the rather common addition of an extra tentacle, the only peculiar specimen found was one which had only three radial muscles and nerves and only eleven tentacles. There were three tentacles in the mid-dorsal interradius (indicated by the mesentery), and four tentacles in each of the lateral interradii.

9. Conclusions.

Probably no theory of echinoderm phylogeny has attracted more attention or seems more plausible than that upon which Semon ('88) determined, as the result of his studies on the development of the auricularia larva of *Synapta digitata.* Although it still finds supporters at the present time, the investigations of Ludwig ('91) on *Cucumaria* and of Ludwig and Barthels ('91) on the anatomy of the Synaptidae have shown the incorrectness of Semon's views, while the observations of Bury ('89 and '95) have cast doubt on his interpretation of some of the conditions in auricularia. It is not my intention to enter here into any discussion of the phylogeny of the echinoderms but only to suggest some of the points in the phylogeny of the holothurians, upon which the history of *Synapta vivipara* seems to throw some light, and to indicate some of the particulars in which my studies have apparently offered support to Bury's ('95) theory of the ancestral form of the echinoderms.

There are three possible opinions concerning the relationship of the Synaptidae to the other holothurians: first, Semon's ('88) view that Synapta represents a primitive form, from which the other holothurians have been derived; second, Cuénot's ('91) view that the Synaptas represent a more primitive branch of the echinoderms than and different from the true holothurians; third, Ludwig's ('89–'92) view that the Synaptidae are degenerate, pedate holothurians. Semon bases his opinion on the high development of the nervous system in Synapta, the absence of anything in their manner of life to cause degeneration, and the fact that no organs appear in the development of the young Synapta which are not present in the adult. His own observations on the nervous system of Synaptas as well as Hamann's ('83) and Cuénot's ('91) show that there is some tendency to diversity in the nervous system, especially as regards sense-organs, among the Synaptidae, and it also shows a considerable degree of adaptability to changing conditions. Moreover, I have found in *S. vivipara* that the sense-organs are highly developed, and there are additional nerves to the oesophagus, indicating modifications to suit the mode of life. It seems from these facts, that too much stress must not be placed on the opinion that the nervous system of *Synapta digitata* is primitive. As regards degeneracy and the absence of anything in the mode of life to cause it in Synaptas, it seems that Semon has expressed an erroneous opinion of the causes of degeneration. He says that we know of only three reasons for its occurrence, parasitic, fixed, or subterranean life, and, since none of these are characteristic of Synaptas, they cannot be degenerate. Had he given the matter more careful consideration he would have seen how untenable his position is. Certainly no one will deny that the loss of the power of flight in certain birds, as the famous New Zealand ground parrot, is degeneration, yet they are neither parasitic, fixed, nor subterranean. Any change in the mode of life, due to a change in environment, may result in degeneracy. The word has come to have a bad significance so that we think of it as indicating that the animal is on the down-hill road, whereas it strictly means that the animal has lost some organ or group of organs which its ancestors possessed and so has become less complex than they. Such a loss must necessarily, however, always be a gain to the species involved, otherwise it could never have come about. Now, it is entirely conceivable that in certain conditions of life on the ocean bottom, in shallow water near shore, the loss of numerous ambulacral appendages and the concentration of the water-vascular system in the circumoral tentacles would be a distinct advantage to the animal. Such has certainly been the case in Caudina (Gerould, '96), for instance, and it is probably true of all the Molpadiidae, although in these cases it may have been brought about by subterranean life. But Semon has by no means proved his point that the Synaptas are not, as a rule, subterranean. Whatever may be the condition at Naples, both on the New England coast and in Jamaica *Synapta inhaerans* and its allied forms are found normally buried deep in the sand, while the large Synaptas, like *S. lappa,* are found under stones, which is practically a subterranean mode of life. The absence of anything, therefore, in their manner of life to cause degeneration is by no means proven and will hardly stand as a good test for considering the Synaptas primitive. The statement that there is no structure developed in the young Synapta which does not appear in the adult is completely refuted by the careful observations of Ludwig and Barthels ('91) on the absence of radial water-canals in the Synaptidae. Since all observers are agreed that radial canals are developed in the embryo of *S. digitata*, it is clear that we have here a most important structure lost in the adult. For these reasons, it seems to me that Semon's view is no longer tenable. Cuénot's ('91) view is based chiefly on the important differences in the embryology of the Synaptidae and that of other holothurians, but it seems to me that he does not take sufficient account of the important evidences of degeneration in the Synaptas.

Ludwig's ('89–'92) view appears to be the one best supported by the facts, and the anatomy and embryology of *S. vivipara* offer no little confirmatory evidence. If we compare its ten-tentacled stage with the hypothetical ancestor which Ludwig describes for the Synaptidae, the resemblance is extraordinary, almost the only important difference being that the genital gland in *S. vivipara* is not equally developed on each side. In fact, the ten-tentacled stage of *Synapta vivipara* represents an actual step in the development of the Synaptidae from Ludwig's hypothetical ancestor. The Jamaican species is beyond doubt a highly modified form, and, though in some respects more highly organized than other Synaptas, in certain particulars, degeneration has gone further. Differing from other holothurians in its manner of life and its mode of reproduction, it has undergone various modifications to fit it for the changed conditions. Living in seaweed near the surface of the water, it has developed pigment in its skin to a marked degree, and at the same time has acquired additional sense-organs in the eyes at the base of the tentacles, and an increased innervation of the oral disc. In conformity to its changed mode of reproduction, important changes have taken place in the structure of the genital gland, openings have appeared in the walls of the rectum to connect the body-cavity with the exterior, while the stone-canal has retained or has acquired secondarily its original connection with the exterior. During the progress of these specializations, the same causes have led to degeneration in other particulars. The changed mode of reproduction has modified the genital duct, so that its lumen is no longer open to the ova, and it no longer has an obvious opening to the exterior. The changed mode of life has caused a greater concentration of the water-vascular system around the mouth and a consequent *further* degeneration of the radial canals, so that they no longer appear as such even in the embryology, but tentacles develop directly from the secondary outgrowths of the hydrocoel. And, furthermore, the mid-ventral outgrowth has degenerated a step further and normally never develops at all, but disappears altogether, which is especially interesting as the mid-ventral radius is the first to develop its nerve and otocysts, and so seems to be the leader in modifications. The manner of life has also caused a modification of the tentacles in a way which we may consider as a degeneration from other Synaptas. Semon ('87) describes calcareous rods in the tentacles of all the Mediterranean Synaptas, and these appear abundantly, as we have seen, in the young stages of *S. vivipara*, but in the adult they seem to have almost entirely disappeared, the tentacles and digits being very delicate and flexible and containing no calcareous deposits, except some miliary granules. The changes in the larva due to the retention and development of the ova in the body-cavity of the mother, such as closing of the blastopore and absence of any true metamorphosis, must also be taken into consideration. For these reasons, we must consider *S. vivipara* as a highly specialized Synapta, but in its water-vascular system it has degenerated a step further than *S. digitata*, although it is neither "parasitic, fixed, nor subterranean" in its manner of life.

It is very clear from the examination of the literature on the subject that the study of any one form or class of echinoderms is entirely insufficient to fit one to determine on a theory of the phylogeny of the group. Notable examples of this may be seen in the speculations of Semon ('88), Bütschli ('92), and MacBride ('96). The *facts* added to our knowledge of echinoderm embryology by all these writers are of real value, but their hypotheses are for the most part of little importance. The same may be said of any attempt to determine the entire course of echinoderm evolution by the study of palaeontology alone, a notable example of which has recently appeared by no less an authority than Haeckel ('96). The only author who has carried on original investigations on all the classes of echinoderms and has formulated his views on the phylogeny of the group is Bury ('80 and '95), and I cannot conclude this paper without calling attention to the support which my observations give to him, on the questions involved in the development of the Synaptidae. Regarding all the points on which he lays particular stress, I have confirmed his work completely or in part. The adradial position of the water-tube, the rudimentary left anterior enterocoel, and the growth of the left body-cavity around the oesophagus are all very clearly marked in the development of *Synapta vivipara*. The only point on which I could not entirely confirm his views was on the formation of the mesentery of the stone-canal from the left coelom entirely, and on this point what evidence I did obtain indicates the correctness of his position.

10. LITERATURE.

[Articles marked * contain references to *Synapta vivipara*.]

Agassiz, A.
'64. On the embryology of echinoderms. Mem. Amer. acad. arts and sci., Vol. 9, p. 1–30.
Baur, A.
'64. Beiträge zur naturgeschichte der Synapta digitata. Nova acta acad. Leop. Carol., Bd. 31, 119 pp., 8 taf.
*Bronn, H. G.
'60. Die klassen und ordnungen der strahlenthiere (Actinozoa). Bronn's Klassen und ordnungen des thierreichs. Leipzig und Heidelberg, 434 pp., 48 taf.
Bütschli, O.
'92. Versuch der ableitung des echinoderms aus einer bilateralen urform. Zeitschr. f. wiss. zool., Bd. 53, suppl., p. 136–160, taf. 9.
Bury, H.
'89. Studies in the embryology of echinoderms. Quart. journ. micros. sci., Vol. 29, p. 409–449, pls. 37–39.
Bury, H.
'95. The metamorphosis of echinoderms. Quart. journ. micros. sci., Vol. 38, p. 45–135, pls. 3–9.
*Clark, H. L.
'96. The viviparous Synapta of the West Indies. Zool. anz., Bd. 19, p. 398–400.
Cuénot, L.
'91. Études morphologiques sur les echinodermes. Arch. de biol., Tom. 11, p. 313–680, pls. 24–31. *See also* Arch. zool. expér., (2), Tom. 9, Notes et Rev., p. 8–16.
Danielssen, D. C., and Koren, J.
'82. Holothurioidea. Norwegian North Atlantic Expedition, 1876–'78. 6. Zoology. Christiania, 94 pp., 13 pls., 1 map.
Gerould, J. H.
'96. The anatomy and histology of Caudina arenata Gould. Proc. Bost. soc. nat. hist., Vol. 27, p. 7–74, 8 pls. *Also* Bull. mus. comp. zoöl., Vol. 29, p. 121–190, 8 pls.
Goette, A.
'80. Bemerkungen zur entwickelungsgeschichte der echinodermen. Zool. anz., Jahrg. 3, p. 324–326.
Haeckel, E.
'96. Die amphorideen und cystoideen. Beiträge zur morphologie und phylogenie der echinodermen. Festschrift zum siebenzigsten geburtstage von Carl Gegenbaur, Bd. 1, p. 1–179, 4 taf.
Hamann, O.
'83. Beiträge zur histologie der echinodermen. 1. Die holothurien (Pedata) und das nervensystem der asteriden. Zeitschr. f. wiss. zool., Bd. 39, p. 145–190, taf. 10–12.
Hamann, O.
'84. Beiträge zur histologie der echinodermen. Heft 1, Die holothurien. Jena, 100 pp., 6 taf.
Hamann, O.
'89. Anatomie der ophiuren und crinoiden. Jena. zeitschr., Bd. 23, p. 233–388, taf. 12–23.
Hérouard, E.
'89. Recherches sur les holothuries des côtes de France. Arch. zool. expér., (2), Tom. 7, p. 535–704, pls. 25–32.
Jourdan, E.
'83. Recherches sur l'histologie des holothuries. Ann. mus. hist. nat. Marseille. Zool., Tom. 1, Mém. 6, 64 pp., pls. 1–5.
Kowalevsky, A.
'67. Beiträge zur entwickelungsgeschichte der holothurien. Mém. acad. sci. St. Pétersbourg (7), Tom. 11, 8 pp., 1 pl.
* Lampert, K.
'85. Die seewalzen. Reisen in Archipel der Philippinen. Von Dr. C. Semper, Bd. 4, Heft 3, 312 pp., pl. 1. Wiesbaden.
* Ludwig, H.
'81. Ueber eine lebendiggebärende synaptide und zwei andere neue holothurienarten der brazilianischen küste. Arch. de biol., Tom. 2, p. 41–58, pl. 3.
* Ludwig, H.
'86. Die von G. Chierchia auf der fahrt der Kgl. Ital. Corvette "Vettor Pisani" gesammelten holothurien. Zool. jahrbücher, Bd. 2, p. 1–36, taf. 1–2.

* Ludwig, H.
'89–92. Echinodermen. Bronn's Klassen und ordnungen des thierreichs, Bd. 2, Abth. 3. Lieferungen 1–16 (Holothurien).

Ludwig, H.
'91. Zur entwickelungsgeschichte der holothurien. Sitzungsber. k. Preuss. akad. wiss., No 10, p. 179–192, No. 32, p. 603–612. *Transl. in* Ann. and mag. nat. hist., (6), Vol. 8, p. 413–427.

* Ludwig, H., und Barthels, P.
'91. Zur anatomie der synaptiden. Zool. anz., Jahrg. 14, p. 117–119.

MacBride, E. W.
'96. The development of Asterina gibbosa. Quart. journ. micros. sci., Vol. 38, p. 339–411, pls. 18–29.

Metschnikoff, E.
'69. Studien über die entwickelung der echinodermen und nemertinen. Mém. acad. sci. St. Pétersbourg, (7), Tom. 14, 73 pp., 12 pls.

Mortensen, T.
'94. Zur anatomie und entwicklung der Cucumaria glacialis (Ljungman). Zeitschr. f. wiss. zool., Bd. 57, p. 704–732, taf. 31–32.

Müller, J.
'50. Anatomische studien über echinodermen. Müller's archiv, Jahrg. 1850, p. 117–155.

Müller, J.
'52. Ueber Synapta digitata und über die erzeugung von schnecken in holothurien. Berlin, 1852, 36 pp., 10 taf.

Örsted, A. S.
'49. [Slaegt of Synapta gruppen.] Videns. medd. nat. for. Kjöbenhavn, Aarene 1849 og 1850, p. vii. *Translated in* Ludwig ('81), p. 48.

Quatrefages, A. de.
'42. Mêmoire sur la synapte de Duvernoy (S. duvernaea A de Q). Ann. sci. nat, Zool., (2), Tom. 17, p. 19–93, pl. 2–5.

Selenka, E.
'67. Beiträge zur anatomie und systematik der holothurien. Zeitschr. f. wiss. zool., Bd. 17, p. 291–372, taf. 17–20

Selenka, E.
'76. Zur entwickelung der holothurien (Holothuria tubulosa u. Cucumaria doliolum). Zeitschr. f. wiss. zool., Bd. 27, p. 155–178.

Selenka, E.
'83. Die keimblätter der echinodermen. Studien ueber entwickelungsgeschichte der thiere. Heft 2, p. 28–61, 6 taf. Wiesbaden.

Semon, R.
'83. Das nervensystem der holothurien. Jena. zeitschr., Bd. 16, p. 1–23, taf. 1–2.

Semon, R.
'87. Beiträge zur naturgeschichte der synaptiden des Mittelmeeres. Mittheil. zool. station Neapel, Bd. 7, p 272–300; p. 401–422, taf. 9, 10, u. 15.

Semon, R.
'88. Die entwickelung der Synapta digitata und die stammesgeschichte der echinodermen. Jena. zeitschr., Bd. 22, p. 175–309, taf. 6–12.

Semon, R.
'89. Die homologien innerhalb des echinodermenstammes. Morph. jahrb., Bd. 15, p. 253–307.

Semper, C.
'68. Reisen im Archipel der Philippinen. 2. Wissenschaftliche resultate. 1. Holothurien, 288 pp., 40 taf. Leipzig.

Thêel, H.
'82. Report on the Holothuroidea. Pt. 1. "Challenger" Reports. Zoology, Vol. 14, Part 13, London.

Thêel, H.
'86. Report on the Holothuroidea. Pt. 2. "Challenger" Reports. Zoology, Vol. 14, Part 39. London.

Thomson, W.
'62. On the development of Synapta inhaerens, O. F. Müller (sp.). Quart. journ. micros. sci., Vol. 2, p. 131–146.

II. EXPLANATION OF PLATES.

[All figures except 20 and 23 were drawn with the aid of a camera lucida.]

ABBREVIATIONS USED.

A. — atrium.
AE. — anterior enterocoel.
AN. — anus.
AO. — atrial opening.
AT. — accessory tentacle.
BC. — body-cavity.
BL. — blastopore.
BV. — blood-vessel.
CF. — ciliated funnels.
CH. — circumoesophageal ring of blood-system.
CM. — circular muscles of body-wall.
CR. — calcareous ring.
CT. — connective tissue.
Car.R. — cartilaginous ring.
Cir.S. — circular sinus formed from the anterior-prolongation of the left coelom.
DV. — dorsal vein of blood-system.
E. — enterocoel.
Ect. — ectoderm.
Epi. — epithelium.
Ey. — eyes.
GD. — genital duct.
GG. — genital gland.
H. — hydrocoel.
I. — intestine.
LC. — left coelom.
LGO. — larval glandular organ.
LM. — longitudinal muscles.
M. — mouth.
Mes. — mesenchyme.
MD. — madrepore.
MY. — mesentery.
NR. — circumoral nerve-ring.
O. — otocysts.
OE. — oesophagus.
OEN. — nerve-band to mouth and oesophagus.
PT. — primary tentacle.
PV. — Polian vesicle.
R. — rectum.
RC. — right coelom.
RN. — radial nerve.
SC. — stone-canal.
SO. — secondary outgrowth of the hydrocoel.
SP. — sense-papilla.
T. — tentacle.
TC. — canal of tentacle.
TN. — tentacle-nerve.
TV. — blood-vessel on inner side of tentacular canal.
V. — valves.
WP. — water pore.
WR. — water-ring.

PLATE 11.

Fig. 1. Mature ovum. 225x.

Fig. 2. Two-cell stage of segmenting egg. 225x.

Fig. 3. Four-cell stage. 225x.

Fig. 4. Eight-cell stage. 225x.

Fig. 5. Sixteen-cell stage. 225x.

Fig. 6. Thirty-two-cell stage, seen from the side. 225x.

Fig. 7. Thirty-two-cell stage. seen from one of the poles. 225x.

Fig. 8. Blastula, seen from the side. 225x.

Fig. 9. Gastrula, seen from the side. 225x.

Fig. 10. Older gastrula, seen from left-hand side, to show formation of the water-pore.

Fig. 11. Still older stage, seen from left-hand side, to show the drawing away of the archenteron from the water-pore. 225x.

Fig. 12. Slightly older stage, seen from left side, to show the formation of the mouth. 225x.

Fig. 13. Older stage, seen from in front (ventrally), to show the formation of the enterocoel. 225x.

Fig. 14. Older stage, seen from in front (ventrally), to show the formation of the coelomic vesicles. 225x.

Fig. 15. Older stage, seen from in front (ventrally), to show the five primary outgrowths of the hydrocoel. 225x.

Fig. 16. Older stage, seen from left side, to show the hydrocoel, body-cavities, and atrium. 225x.

Fig. 17. Very young pentactula, from right side, to show the nerves and sense-organs. 225x.

Fig. 18. Older pentactula, seen from dorsal surface, to show the radial nerves, calcareous ring, and rudiment of accessory tentacle. 130x.

Fig. 19. Ten-tentacled young, seen from right side, to show genital gland and arrangement of organs. Twelfth tentacle just developing. 22x.

Fig. 20. Adult *Synapta vivipara*, seen from ventral surface. Nat. size.

PLATE 12.

Fig. 21. Vertical section of gastrula, to show the thickened ectoderm at apical pole. 225x.

Fig. 22. Transverse section of Fig. 13, at the line A. B., to show the thickened ventral ectoderm. 225x.

Fig. 23. Schematic outline of hydrocoel, to show the position of water-canal.

Fig. 24. Transverse sections of hydrocoels of three embryos, to show formation of anterior enterocoel. *a*, youngest stage; *b*, somewhat older; *c*, oldest stage. 225x. In *c*, only a very small part of the hydrocoel is shown.

Fig. 25. Transverse section of larva, somewhat older than Fig. 16, to show closure of hydrocoel ring, without the formation of a Polian vesicle. 225x. The section is very oblique, and takes in a part of the floor of the atrium (A), and only a portion of the hydrocoel.

Fig. 26. Transverse section of larva like Fig. 16, to show anterior prolongation of the left coelom. 225x.

Fig. 27. Transverse section of same larva, somewhat higher up, to show the left prolongations of the left coelom. 225x.

Fig. 28. Longitudinal section of larva like Fig. 16, very badly preserved, to show the anterior prolongation of the left coelom, *ant. l. c.* 225x.

Fig. 29. Posterior end of an adult, to show the rupture of the body-wall, caused by birth of the young. 35x.

Fig. 30. Transverse section of the posterior end of an adult, to show one of the openings from the rectum into the body-cavity. 65x.

Fig. 31. One of these openings more highly magnified. 500x.

Fig. 32. Part of a transverse section of a young pentactula, to show the origin of the genital gland. 500x.

Fig. 33. Similar section of an older larva, to show the increased development of the genital gland. 500x.

Fig. 34. Similar section of a still older larva, to show first appearance of lumen and covering epithelium of the genital gland. *l*, beginnings of lumen; *epi*, outer epithelium of gland, formed secondarily from right side of mesentery. 500x.

Fig. 35. Similar section of a young twelve-tentacled larva, to show the genital gland well developed on the right-hand side of mesentery and confined to that side. 500x.

Fig. 36. Part of a similar section of an adult, to show the formation of the lumen of the genital duct from the lumina of the glands. 200x.

Fig. 37. Longitudinal section of a part of genital duct, to show its structure and [illegible] duct; *g. e*, germinal epithelium, *m. e*, epithelium of mesentery. 950x

Fig. 38. Transverse section of dorsal body-wall of an adult, to show the [illegible] matozoa. 225x.

Fig. 39. Longitudinal section of a small part of genital gland, to show the [illegible] thelium of the gland. *ep*, epithelium of gland, *ov*, ovum 500x

Fig. 40. Transverse section of genital gland, to show its structure and the [illegible]

PLATE 13.

Fig. 41. Transverse section of the ectoderm of a pentactula, to show the invagination which forms the larval glandular organ. 500x

Fig. 42. Transverse section of the same organ, fully grown, from the body-wall of a ten-tentacled larva. 500x.

Fig. 43. Longitudinal section of one of these organs, to show the peripheral position of the nuclei, and the lumen at the center. 500x.

Fig. 44. Interradial plate from the calcareous ring of an adult. 35x.

Fig. 45. Radial plate from the same ring. 35x.

Fig. 46. The development of these calcareous plates. *a*, youngest stage; *b-g*, successively older stages; *n*, older stage of an interradial plate; *i*, older stage of a radial plate. 225x.

Fig. 47. Part of the calcareous ring of an old ten-tentacled larva, to show the growth of the radial plate (*r.p.*) of the calcareous ring, in support of the developing eleventh tentacle. *ip*, interradial plates. 65x.

Fig. 48. Calcareous rods from the tentacles of a ten-tentacled larva. 225x.

Fig. 49. Calcareous rods from around madrepore. 225x.

Fig. 50. Miliary granules from the skin of an adult. 225x.

Fig. 51 Anchor from the skin of an adult 120x.

Fig. 52. Normal anchor-plate from an adult. 120x.

Fig. 53. Abnormal anchor-plate from an adult. 120x.

Fig. 54. Longitudinal section of the tentacle of an old pentactula, to show the thickened ectoderm at the tip. 225x.

Fig. 55. Cross-section of a young tentacle, to show the entire separation of the canals of the digits from the central canal of the tentacle. 225x.

Fig. 56. Longitudinal section of part of a young tentacle, to show the origin of the digits, as outgrowths of the tentacle-canal. 225x.

Fig. 57. Tentacle of an adult. 22x.

Fig. 58. Transverse section of a mesentery and intestine of a pentactula, to show the origin of the haemal system from the right lamina of the mesentery. 500x.

Fig. 59. Loop of intestine in a small adult, to show formation of the transverse vessels of the haemal system. 35x.

Fig. 60. The same from an older specimen. 65x.

Fig. 61. Cross-section of the dorsal mesentery of a larva one mm. long, to show the beginning of the ciliated funnels. 575x.

Fig. 62. The development of the ciliated funnels. *a*, the first large cells seen from above looking down on the surface of mesentery; *b*, increased number of cells; *c*, slightly older stage seen from the side; *d*, older stage, surface view; *e*, older stage, seen partly from the side; *f*, older stage seen from the side. 575x.

Fig. 63. Longitudinal section of a funnel, to show its structure. 950x.

Fig. 64. Ciliated funnel of an adult, seen from in front. 575x.

Fig. 65. Ciliated funnel of an adult, seen from above. 225x.

Fig. 66. Surface view of stone-canal of an adult, to show its course from water-ring to the exterior. 35x

PLATE 14.

Fig. 67. Cross-section of stone-canal and genital duct of an adult before they enter the body wall. 225x.

Fig. 68. Cross-section of stone-canal and genital duct of same adult in the body-wall. 225x.

Fig. 69. Cross-section of same stone-canal as it approaches the body-wall. 225x.

Fig. 70. Cross-section of the same, where it opens to the exterior. 225x.

Fig. 71. Cross-section of the terminus of a stone-canal with two openings, to show the uppermost opening. 500x.

Fig. 72. Cross-section from the same series, two sections lower down. 500x.

Fig. 73. Cross-section of the same series, two sections further down, to show the second opening. 500x.

Fig. 74. Cross-section of a stone-canal of an adult, taken through the madrepore to show the openings. 225x.

Fig. 75. Longitudinal section of nerve-ring of an adult (transverse section of the animal), to show the nerve-band to the mouth and oesophagus in cross-section. 200x.

Fig. 76. Transverse section of nerve-ring (longitudinal section of animal), to show the same nerve in sagittal section. 200x.

Fig. 77. Longitudinal section of nerve-ring and transverse section of tentacle-nerve, to show the position of the eyes. 120 x.

Fig. 78. Cross-section of nerve-ring and one of the eyes, to show their relative position. 225x.

Fig. 79. Cross-section of the tip of one of the eyes, to show the vacuolated structure of the mesenchymatous covering as well as of the polygonal nerve-cells. 950x.

Fig. 80. Sagittal section of one of the eyes, to show the shape and structure of the nerve-cells. 950x.

Fig. 81. Cross-section of an otocyst and its single vesiculated cell from a pentactula. 500x.

Fig. 82. Cross-section of the otocysts and a part of the radial nerve from a twelve-tentacled young five mm. long. 500x.

Fig. 83. Cross-section of an otocyst of an adult, showing the single vesiculated cell within. 500x.

Fig. 84. Cross-section of a sense-papilla in the ectoderm of an adult, to show its structure and nerve connections. *ga*, ganglion; *n*, nerve running to radial nerve. 500x.

PLATE 15.

Fig. 85. Transverse section of an old pentactula, to show the formation of the five accessory tentacles and the otocysts; the secondary outgrowths of the left dorsal and mid-ventral radii have not developed at all as yet. The section is slightly oblique, more posterior on the left than on the right. 225x.

Fig. 86. Transverse section of an old ten-tentacled stage, to show position of the eleventh and twelfth tentacles. The section is somewhat oblique, more posterior on the right than on the left. 120x.

Fig. 87. Longitudinal section of the anterior end of a pentactula; on the left through a radius; on the right a little to one side of a radius. *f*, indicates the place of fusion between the oesophagus and roof of the atrium. 225x.

Fig. 88. Another section of the same series; on the right, through an interradius, just touching on the side of the Polian vesicle; on the left a little to one side of an interradius. *f*, indicates the fusion of the oesophagus with the roof of the atrium. 225x.

Fig. 89. Longitudinal section of a ten-tentacled young, to show position of the various organs. 65x.

Fig. 90. Longitudinal section of an adult through one of the tentacles, to show the position of the various organs. 35x.

Fig. 91. Longitudinal section of an adult through a radius, to show position of the organs. 35x.

Fig. 92. Adult laid open in right dorsal radius, to show position of the organs and especially the blood-vessels on digestive tract. Nat. size.

Fig. 93. Larval monstrosity, a double embryo. 225x.

Fig. 94. Cross-section of longitudinal muscle of adult at the point of juncture with the calcareous ring. 65x.

Fig. 95. Cross-section of same muscle, lower down. 65x.

Fig. 96. Cross-section of same muscle, lower down. 65x.

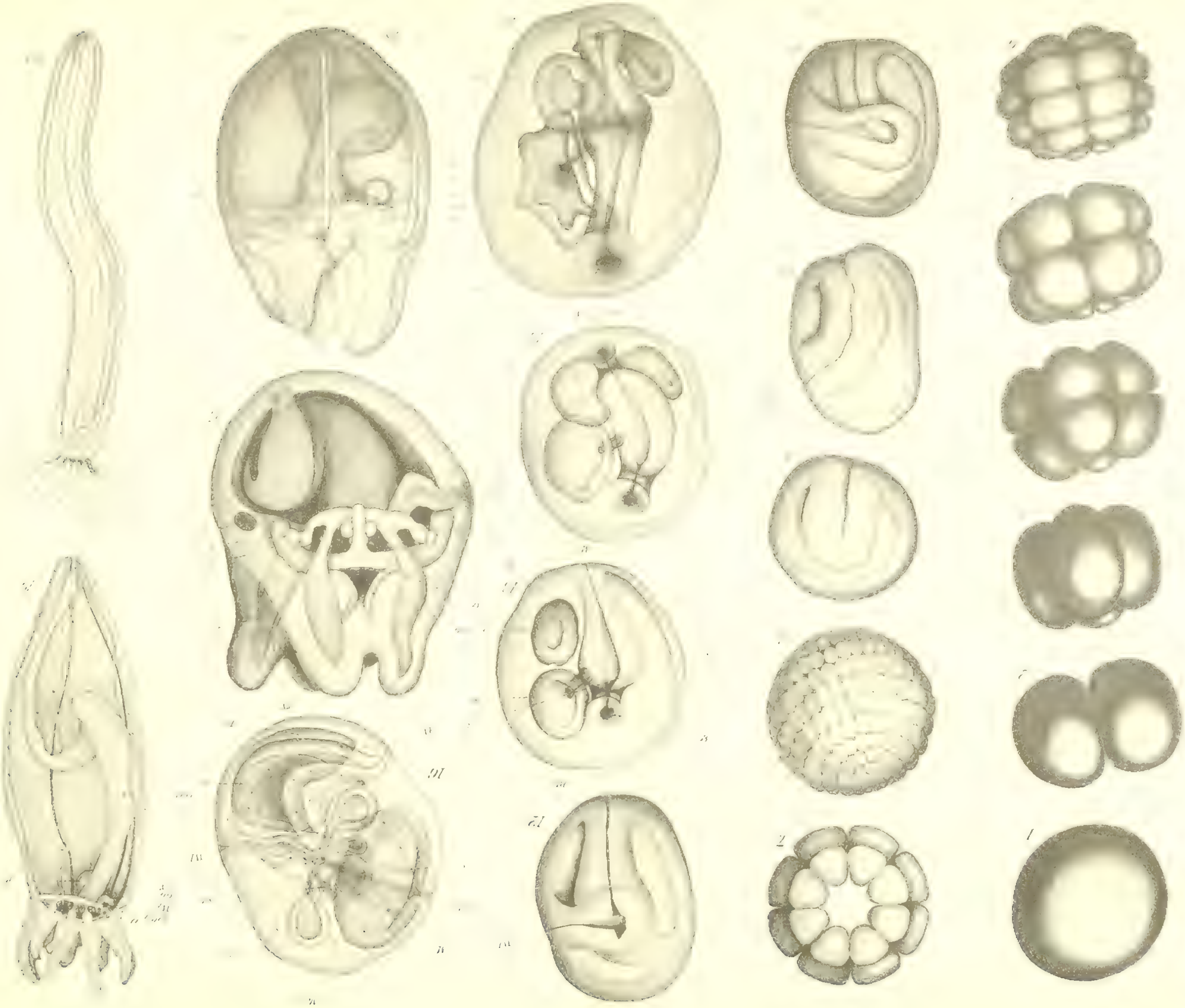
Fig. 97. Cross-section of same muscle, lower down. 65x.

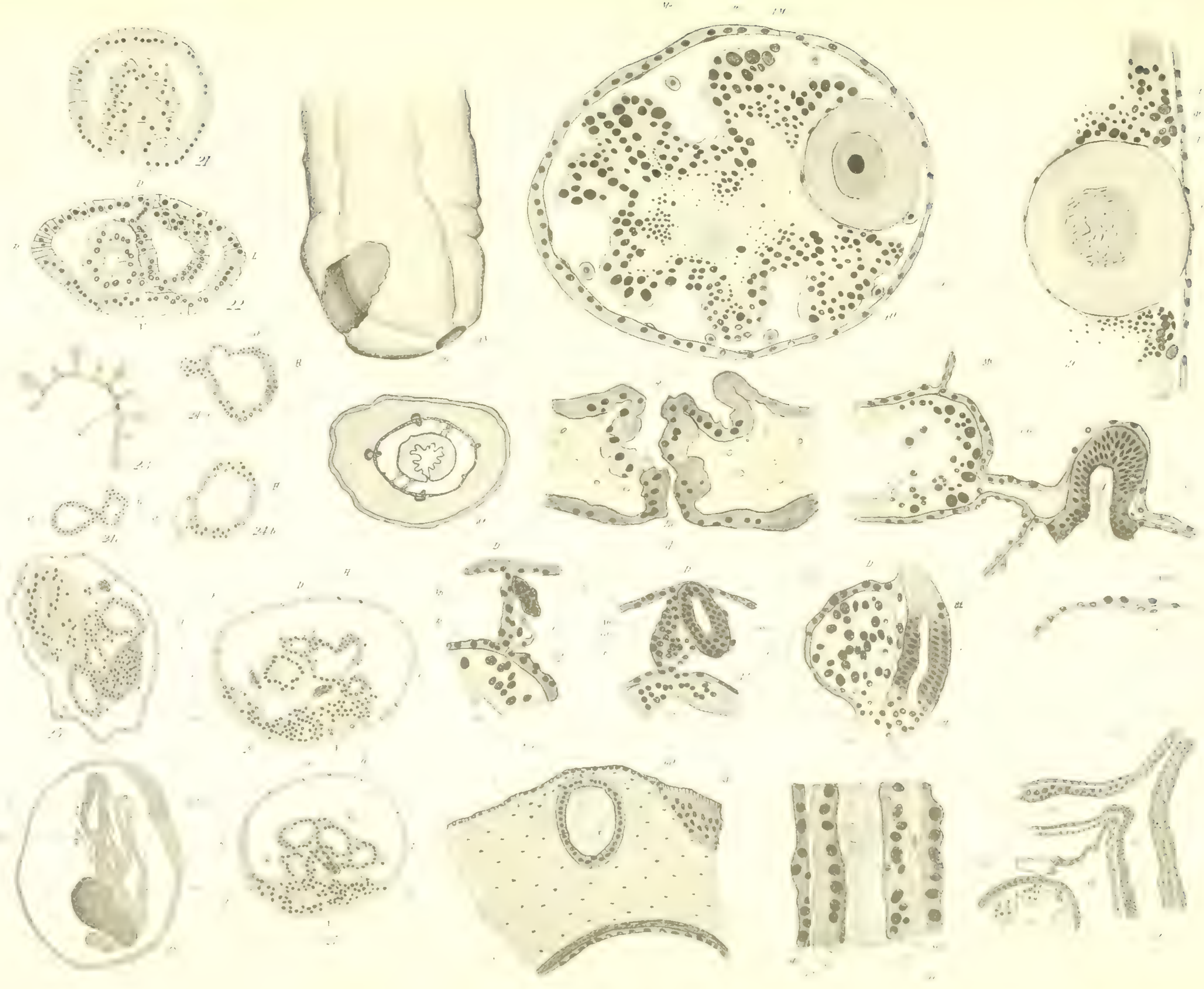
Fig 98. Cross-section of longitudinal muscle of a smaller adult, somewhat anterior to the middle of the body. 200x.

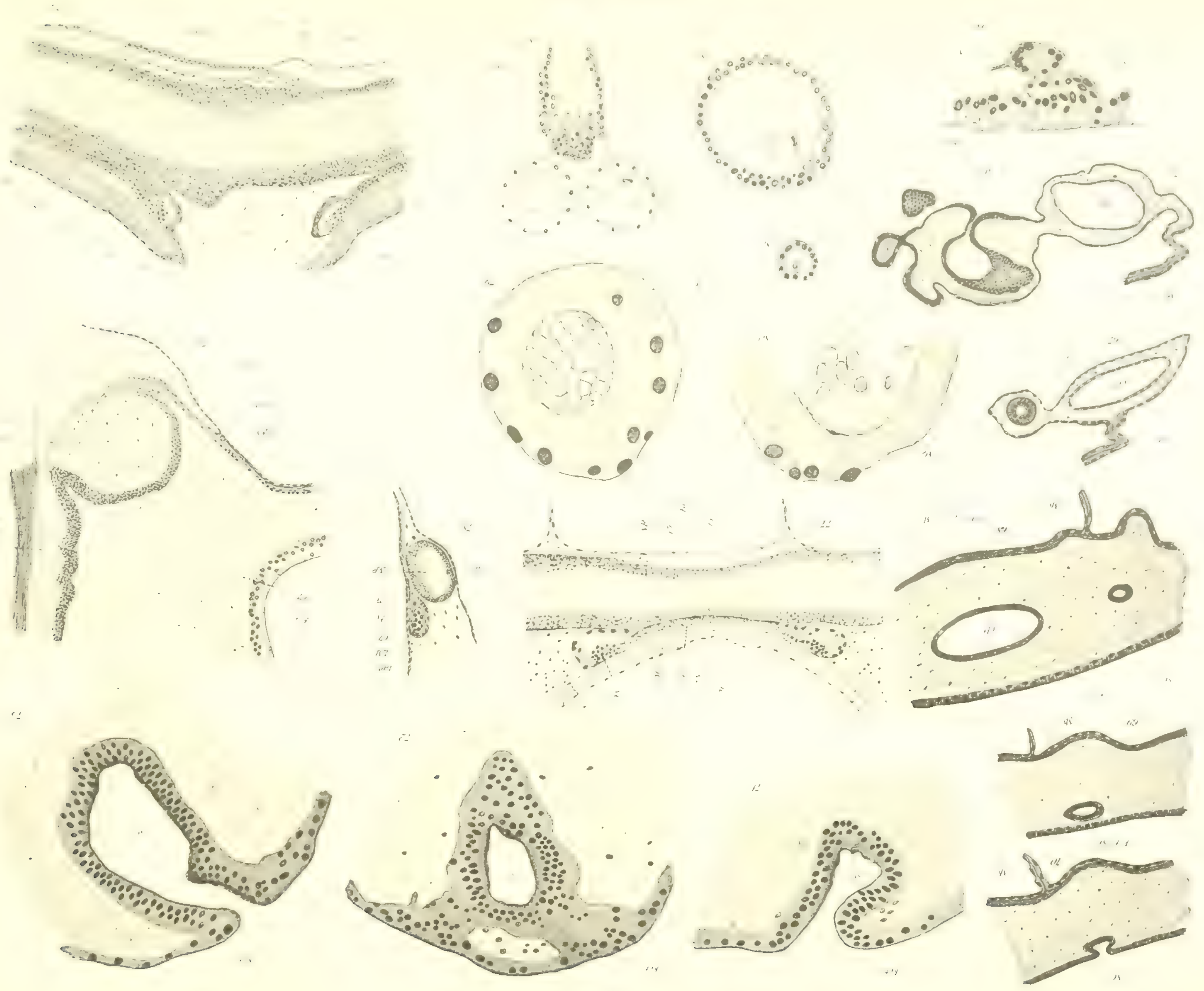
Fig. 99. Cross-section of a longitudinal muscle in the middle of the body. 80x.

Fig. 100. Cross-section of a longitudinal muscle at extreme posterior end of the body. 200x.

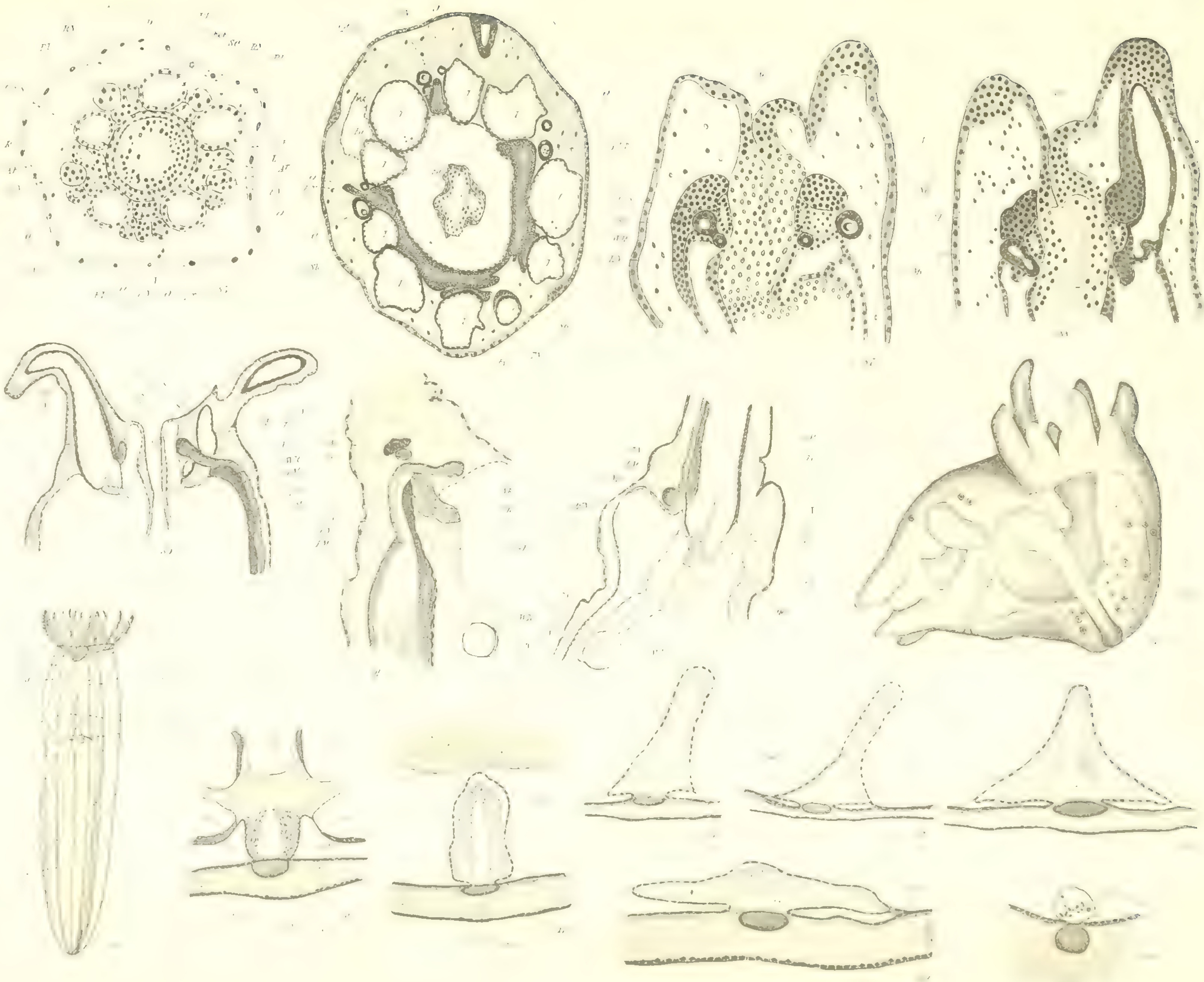
Printed, January, 1898.


1
7
12
16


21
D
22
24b
24c



[illegible]



4. LOCALIZED STAGES IN DEVELOPMENT IN PLANTS AND ANIMALS.

BY ROBERT TRACY JACKSON.

(Read November 2, 1898.)

IN this paper growth is considered in its limitation as mere increase in bulk, without addition of differential characters. Development, on the other hand, is used in the sense of implying differentiation, either progressive or regressive.

In the ontogeny of animals, stages in development have long been recognized, and their elucidation has been attained in numerous researches. Von Baer was one of the first to recognize the fact, that early stages of the embryo resemble the adult condition of simpler forms in the animal kingdom. Louis Agassiz accepted this view, and greatly enlarged it. Professor Agassiz ('63) gave full expression to the view, that stages found in the ontogeny of the individual represent, in an epitomized form, the adults of simpler types of the group to which the animal belongs. He first recognized the important principle that the succession of stages in development of the individual represents, in an abbreviated form, a series of adult more primitive types, and that this series of primitive types appeared in geological succession in the same progressive order in which the representative stages appear in the ontogeny of the individual.

The important law of stages in ontogenesis was formulated by Prof. Alpheus Hyatt as follows: *In the young, stages are found, the equivalents of which are to be sought in the adults of ancestral types.*

While the earliest stages in development have been extensively studied by embryologists, later or post-embryonic stages, on which Professor Agassiz laid especial stress, have been generally overlooked. It is for the most part in recent years that these later stages have received the attention that is their due. The study of later stages has been the principal method of research by Hyatt, Beecher, Clarke, Schuchert, Smith, the author, and others. From this method of study important results have been attained in our knowledge of the filiation of several groups of invertebrates.

From his researches Professor Hyatt discovered the fact, that in the old age of the individual, stages may also be found. These senile stages recall in a broad way the somewhat similar stages seen in the young. Successive senile stages, however, when repeating larval or adolescent stages, do so in the inverse order of succession from that of their appearance in the young. Senile stages are prophetic of types which may be found in regressive series of the group to which the animal belongs, as shown by Hyatt in cephalopods and by Beecher in brachiopods. Senility is marked by the loss or reduction of those characters which are fully evinced in the adult as specific and generic characters, and by the taking on of features of its own period of growth.

To quote Hyatt ('97), "The cycle of the ontogeny is, therefore, the individual expression and abbreviated recapitulation of the cycle that occurs in the phylogeny of the same stock; and, while the embryonic, nepionic, and neanic stages give us, in abbreviated shape, the record of the epacme, the gerontic stages give, in a similar manner, the history of the paracme." Professor Hyatt formulated the law of senile characters as follows: *In the old age, stages are found, which are similar to stages found in the young, and are prophetic of types to be found in degradational series of the group to which the animal belongs.*

The above principles and their application, Hyatt's and Cope's principle of acceleration of development, the well-known principles of parallelism, and the dynamic relations of the organism to its environment of Cope, Hyatt, and Ryder, form the central working principles of Prof. Alpheus Hyatt and his followers, and may be justly termed the Hyatt school. The principle of localized stages in development as described in this paper is in the direct line and the natural outcome of this method of work.

Studying organisms in accordance with the above laws, one expects to find stages, in a more or less marked degree, in the immature organism and also in the old age. In the adult one expects to find the full species characters evinced, and, excepting as the adult represents one step in a chain of organic series, stages are not looked for.

From observations on animals and plants, evidence has been obtained which points to the conclusion, that, in addition to stages in the young, and in the old age, stages may be found in localized parts throughout the life of the organism.

In organisms that grow by a serial repetition of parts, it is found that there is often an ontogenesis of such parts, which is more or less closely parallel to the ontogenesis of the organism as a whole. In the ontogeny of such localized parts in a mature individual, we find stages in development during the growth of the said parts which repeat the characters seen in a similar part in the young individual. To state it briefly for the moment, such localized stages have been observed in the leaves of plants, in branches or suckers of plants, in the budding of some lower animals, as Hydra and Galaxea, in the plates of crinoids and Echini, in external ornamentations in mollusks, and in the septa of cephalopods.

Localized stages in development must be clearly differentiated from stages in development of the organism as a whole. They are features seen in localized parts throughout the life of the individual, or are capable of being brought into existence by certain conditions throughout the life of the individual. Localized stages are essentially features of the adult, although they may be evinced earlier or later than what would technically be considered as the ephebic period.

In Strassburger's Botany ('98) occurs a statement which is to the point in the present studies. It is as follows: "Whatever is true of the development of a plant from the embryo, is also, as a rule, applicable to its further growth from the growing point, and, consequently, a knowledge of the mode of development at the growing point is of great importance in detecting homologies." The same principle is applicable to many animals.

As stages found in the young repeat the characters of ancestral forms, so stages found in localized parts repeat the characters of ancestral forms, and their adult equivalents are to be sought in more primitive, sometimes more specialized, living or fossil allies. From localized stages we may gather suggestive clews to the phylogeny of a group.

Localized stages have an important bearing on the study of variation. In the arrested or specialized development of a localized part, characters may be seen which are comparable to more or less exceptional individuals, where the whole organism has an arrested or otherwise modified character. The localized and the individual variation may be reversionary or progressive in the line of variation of the group, and comparable to fossil or living, ancestral or specialized members of the group. From this point of view, localized stages deserve careful study. Besides atavic and progressive variation, aberrant variation as well as parallelism may be represented in localized or individual variation. To which class of variations a given character belongs, cannot usually be safely assumed without a study of the young and related forms both living and fossil.

In studying localized stages of development, it is found that there are certain general methods of their expression which should be considered. In the ontogeny of a localized part, the stages may be transitory, and only seen if the part is observed at a certain period of its growth. Such are the earlier stages in the growth of individual leaves, the simple leaves at the base of suckers of many plants, as oaks, ashes, Ailanthus, the simplest condition of budding corals and of the plates of crinoid stems and Echini. On the other hand, localized stages in development may be permanently retained in certain areas of the part. Cases of such local permanent retention of primitive features are the distal tips of leaves which resemble the whole leaf of the young, as seen in the Tulip-tree and in the compound leaves of Ailanthus, ashes, Phoenix, Areca, Pteris; or the proximal portion of the leaf may repeat the character of the simpler condition, as in Gymnocladus. The septal sutures of Ammonites retain permanently on their inner umbilical border a simpler condition.

The portion of the organism which is represented in the localized stage may be more or less extensive. It may be reduced to a single part, as a leaf or even a portion of a leaf of a plant, or a plate of an echinoderm; or it may include a series of parts in which localized stages are observable, as in suckers of plants, certain portions of a branch (Larch), and diseased, reversionary, or otherwise modified branches of plants (Red Cedar, Tuliptree). It is obvious that this latter distinction is only a modification of the first, but yet is convenient to maintain.

Localized stages may be developed in the natural growth of the individual, or they may be evinced only under more or less abnormal or pathologic conditions. Cases of this are reversionary suckers in the Pitch Pine, suckers developed on the felling of trees, growths on mutilated branches of Liriodendron and Ailanthus, tuft-like branches of the Red Cedar with acicular leaves.

Youthful or reversionary features may be developed only at certain definite areas of the organism. Such are compound leaves at the base of *Ampelopsis tricuspidata*, ovate leaves on the current season's growth of the same, arrangement of leaves on the current season's growth in the Larch. In general, suckers from the base of the trunk or roots of trees have a strong tendency to reproduce nepionic or reversionary characters.

If there is truth in the principle of localized stages in development, from them we should be able to predicate with some accuracy the conditions of the young, and concurrently of ancestral types as well. I think that this may be done. The existence of localized stages was first observed in Palaeozoic Echini and was published in Studies of Palaeechinoidea ('96, p. 228).

The occurrence of localized stages, and their bearing, may be expressed in the following law, which should be compared with the laws concerning youthful and senile stages: *Throughout the life of the individual, stages may be found in localized parts, which are similar to stages found in the young, and the equivalents of which are to be sought in the adults of ancestral groups.* While this law covers the usual conditions, it is possible and even probable that degradational or progressive features may appear as localized stages. To include such cases the following clause may be added: *The equivalents of regressive or progressive localized stages are to be sought in the adults of degradational or progressive series of the group.*

My sincere thanks are due to Mr. Charles E. Faxon of the Arnold arboretum, Harvard university, for reading the manuscript of the botanical portion of this paper, and for helpful suggestions on the same, also for aiding me with material. For seedlings and other material, studied at the Arnold arboretum, my thanks are due to Prof. Charles S. Sargent, Director of the Arboretum. For many seedlings valuable in my studies I am indebted to the kind interest of Miss Marian C. Jackson, the Shady Hill nurseries of Bedford, Mass., and others as mentioned in the text.

Localized Stages in Development in Plants.

In many cases in the following pages simple stages in the development of seedlings are described, often in considerable detail, but these are not to be confused with localized stages in development which are compared with them. Sir John Lubbock's work on seedlings has been a great help and is frequently referred to.

In the nomenclature of stages in development of animals, the term nepionic is applied to stages immediately succeeding the embryonic. The term has not been applied before to plants, but as cotyledons are the last of the truly embryonic features, the immediately succeeding growth is considered as the nepionic stage.

In the higher plants the tip of the leaf is formed first, and usually growth ceases early at that point, it being transformed into permanent tissue (Sachs, '75). Such being the fact, it is evident that the proximal portion of the leaf is formed last. The tip of the leaf should be the most primitive portion, and the proximal portion, usually at least, the most specialized portion, as is shown to be the fact in many cases in the following pages. If a leaf undergoes an arrested development from any cause, the distal tip at least will be formed, and the proximal portion will fail to develop or will be modified in varying degrees. In progressive evolution newly added characters will be likely to make their appearance at the proximal end of the leaf. As a corollary, in regressive evolution, regression will tend to be evinced by a dropping out of characters at the proximal end of the leaf.

Aquilegia canadensis. In the seedling columbine, *Aquilegia canadensis* L. (Pl. 16, fig. 16), the cotyledons are broadly rounded, with long petioles and a slight emarginate distal notch. The first nepionic leaf is trifoliolate, the median leaflet having two marked notches, and each of the lateral leaflets one slighter notch on the lower side. Later nepionic leaves are similar. In the adult (Pl. 16, fig. 17) the leaf has three branches. The two lateral divisions are trifoliolate and repeat the form of the median division. The terminal division is trifoliolate, like the whole nepionic leaf. The median leaflet has two major clefts, comparable to the two indentations of the median leaflet of the nepionic leaf, and the two lateral leaflets each have a major cleft on the lower side, comparable to the notches of the lateral leaflets of the nepionic leaf. While the adult leaf has relatively deeper notches and in addition has minor dentations, we may see, in the leading features of the terminal leaflet, a repetition of the characters of the whole nepionic leaf of the seedling.

Liriodendron tulipifera. In the Tulip-tree (*Liriodendron tulipifera* L.) the seedling (Pl. 16, figs. 8, 11) has simple lanceolate cotyledons. The first nepionic leaves are alternate, distally emarginately truncate, rounded for the rest of their outline. The angle between the truncation and curved sides in the first nepionic leaves is rounded, but in later leaves becomes comparatively sharp, as shown in different leaves of the specimens figured. The third nepionic leaf of Fig. 11 has slight emarginate lobes, the beginning of the lobes which are characteristic of the species. Gradually during later growth the typical form of leaf of the species is built up. In young trees, up to six or ten feet in height, the leaves, as observed in many cultivated specimens, are large and vigorous and four-lobed (Pl. 16, fig. 1), no six-lobed leaves having been observed in such individuals.

In the adult tree the typical leaves are four- or six-lobed (Pl. 16, fig. 12). Six-lobed leaves are figured in Professor Sargent's Silva as the characteristic leaves, and although they are in some individuals uncommon or absent, they are usually abundant in adult trees, as far as my observations have gone. It should also be said that four-lobed leaves are abundant on all typical trees. When four- and six-lobed leaves occur on the same branch, the six-lobed leaves are on the proximal end, and four-lobed leaves on the distal portion, showing this definite relative position in the cases observed.

In this species the leaves are very variable, but in all variations the distal truncation is never departed from, this distal portion of the leaf (as noted in many other cases) always retaining the character which is evinced in the young nepionic leaves. Variations are especially noticeable in late or feeble growths, especially at the ends of branchlets, but may occur as isolated individual leaves on any part of the branch. In Pl. 16, fig. 13, is represented a characteristic variation of the tip of a branch from the same tree as Fig. 12. Leaf 1 has two lateral sinuses moderately developed, a little more so than leaf 3 of Fig. 11, but similar to the characteristic form seen in somewhat older seedlings. Leaf 2 has very slight lateral sinuses, and leaf 3 is a close approach to leaf 1 of the seedling (Fig. 11). In Pl. 16, fig. 4, is represented a small reversionary leaf from the same tree, which is similar to leaf 4 of the seedling (Fig. 11). On the same tree a branch had been mutilated by browsing cattle, and a weak late growth (July) was thrown out. Two of these leaves are represented in Pl. 16, fig. 7. One leaf has slight marginal sinuses, the other is entire, both closely resembling leaves of the young seedling (Fig. 11). All of these aberrant leaves are seen to be distinctly reversionary in character, closely resembling the condition seen in an early stage of the seedling. According to the views expressed, these may be considered as leaves which have undergone an incomplete development and are reversionary through a failure in their individual ontogeny to develop full specific characters.

In adult *Liriodendron tulipifera* leaves are occasionally found which have eight lobes (Pl. 16, fig. 3), there being two small marginal lobes in addition to the six lobes characteristic of the species. Holm ('90) has also described eight-lobed leaves, and my figure is taken from that author. These leaves have developed more than the full specific characters and would tend to show what may be expected as the next step in the evolution of the type, provided additional species are differentiated in the progressive line of evolution of the group.

Besides reversionary leaves, reversionary individuals are not uncommon in this protean species. Frequently trees are seen in which all the leaves are four-lobed (Pl. 16, fig. 1), similar to a stage attained early in an individual which has six-lobed leaves in the adult. At the Arnold arboretum, there is an interesting tree which is highly reversionary in character. All or essentially all of the leaves are rounded, distally truncate, with slight angles at the lateral terminations (Pl. 16, fig. 10), closely resembling the nepionic leaves of the seedling (Pl. 16, fig. 11, leaf 4). A branch of this tree which shows a progressive localized variation is represented in Pl. 16, fig. 9. It is progressive for the individual because more specialized than the typical leaves, although if it were on a normal tree of the species it would be a regressive variation. Leaf 1 has one slight lateral lobe on the middle half of each side; leaf 2 has two slight lateral lobes corresponding to the two well-developed lobes of a normal tree (Fig. 12). Leaf 3 is nearly orbicular, truncate, reversionary, and comparable to early leaves of seedlings. A tree with similar leaves in the Botanic garden in Washington was described by Holm ('90). On Pearl street, Dorchester, Mass., there is a tree in which the typical leaves have six slightly developed lobes as in leaf 2 (Pl. 16, fig. 9). In another tree at the Arnold arboretum, the typical leaves are four-lobed as in Fig. 1. This is not an uncommon variation, as noted, and many such leaves occur on all typical trees. It bears a close resemblance to *Liriodendron giganteum* Lesq., of the Cretaceous.

In the development of *Liriodendron tulipifera*, there is a distinct progressive series of leaf differentiation. Starting with the young seedling, we find first a leaf which is rounded, distally truncate (Pl. 16, fig. 5); next the terminal angles become sharpened (Fig. 6); then lateral lobes become gradually differentiated, at first slightly, then strongly marked (Fig. 1); then two additional lobes appear (Figs. 2 and 12), giving the full specific characters. As a variation in the direct line of progressive differentiation, two more lobes may be differentiated (Fig. 3). In regressive leaves at the tips of branches, etc., as described, these same characters are repeated, but in inverse order, a slightly regressive leaf drops out the two basal lobes (Fig. 2 a–b), a more regressive leaf drops out two more lobes (Fig. 2 c–d), an extremely regressive leaf becomes rounded at the angles (Fig. 2 e–f) and repeats the characters of young seedlings. It is seen that progressive development proceeds by adding characters at the proximal end of the leaf, and regression is marked by the dropping out of characters at the proximal end. The distal end never suffers any considerable change.

Turning to the fossils, we find that *Liriodendron primaevum* Newb., of the Cretaceous, is an ancient form which has a rounded leaf, distally truncate, resembling the leaves of the young seedling (Fig. 8). *Liriodendron meeki* Heer, of the Cretaceous, has slight marginal sinuses, being quite close in form to leaves in late growth of seedlings, or regressive leaves of adults (Fig. 13, leaf 1). In *Liriodendron giganteum* Lesq., from the Cretaceous, the leaf is four-lobed, with well-developed sinuses, and resembles leaves of young trees, or four-lobed leaves of adults (Fig. 1).

Holm ('90) has questioned the validity of these fossil species, because variations equivalent to them may be found in our modern species. His objection may be met by the reasonable supposition that, in fossilization, only the average leaves of the tree stand any probable chance of preservation. Aberrant leaves, in virtue of their small number, stand relatively a slight chance of preservation as fossil representatives of ancient floras.

AILANTHUS GLANDULOSA. In *Ailanthus glandulosa* Desf. the seedling (Pl. 16, fig. 15) has broad, rounded cotyledons of leathery consistency. The first two nepionic leaves are opposite, compound, composed of three leaflets each. The terminal leaflet is lanceolate, the lateral leaflets have entire margins. Succeeding leaves are alternate in arrangement. They are also trifoliolate, but soon more leaflets are added. A specimen seven inches high has seven leaflets on the youngest or last added leaves. Part of the leaflets of the two upper leaves of Pl. 16, fig. 15, have already acquired slight notches, which are a characteristic feature of adult leaves. According to Lubbock ('92) the first nepionic leaves of *Ailanthus glandulosa* var. *rubra* are also trifoliolate.

The adult *Ailanthus glandulosa* has very large compound leaves, imparipinnate, with about 25–33 leaflets. The distal ends of the leaves closely resemble the first nepionic leaves of seedlings, differing principally in the added marginal notches. In an adult tree in Cambridge, at a point where a branch had been broken, a weak late growth was thrown out. In this growth all the leaves had few leaflets, and one leaf had only three; therefore, excepting for its marginal notches, repeating the characters of the first nepionic leaf of the seedling. In all of these depauperate leaves the terminal and other leaflets were similar to those seen at the ends of normal adult leaves. The reduction was in the suppression of the proximal portion of the leaf, or that portion which is formed last in the ontogenesis of the leaf.

This species suckers freely from the roots, suckers often appearing at a considerable distance from the base of the trunk. Suckers at first usually have simple leaves (Pl. 16, fig. 14), though occasionally the first leaves seen were trifoliolate. These simple leaves are alternate, ovate, elongate, similar to, but relatively shorter than, the distal leaflet of the leaves of seedlings. Succeeding the simple leaves are compound leaves, first trifoliolate, later with more leaflets, the leaves all being alternate in arrangement. It is a striking fact, the only case so far seen, that the suckers are simpler, more primitive than the seedling. Whereas the seedling starts with opposite trifoliolate nepionic leaves, the sucker begins with alternate simple leaves. In the Ailanthus then we find nepionic characters repeated in suckers and regressive leaves of feeble growths.

Rhus toxicodendron. The seedling of the Poison Ivy (*Rhus toxicodendron* L.) has two evenly rounded, fleshy cotyledons (Pl. 16, fig. 18). The first nepionic leaves are trifoliolate and opposite. Succeeding leaves are similar but alternate. The terminal leaflet has a short stalk, but lateral leaflets are sessile as in the adult. Lateral leaflets of these early leaves present a small lobe on their proximal borders. The leaves of the adult differ little from those of the seedling except in the lengthening of the stem of the terminal leaflet and the usual absence of lobes on lateral leaflets. While this is true at West Chop, Mass., where the soil is barren, in fertile soils growth is more luxuriant and lobation is commoner. Also in vigorous adults there may be several lobes instead of a single lobe in individual leaflets. Simple leaves are occasionally seen in adults. Leaves near the base of the adult vine (nepionic area) have a tendency to produce lobed leaves similar to those of the seedling. In seedlings grown in fertile soil nepionic leaves are occasionally more lobate than in the specimen figured. Lateral leaflets may have two lobes and the terminal leaflet a lobe on either side. Such extra lobation is not common, however, and the specimen figured is typical of most of the seedlings seen. Primary (nepionic) leaves in this genus show considerable variation, according to Lubbock ('92) being scale-like, simple, or, as he says in one species, *Rhus typhina*, trifoliolate. In *R. toxicodendron*, the trifoliolate nepionic leaves, so similar to those of the adult, mark it as a species with an accelerated development, a feature common in degradational species. The degradational or specialized character of this species is indicated by its creeping habit, its development, and perhaps by its toxic properties as well.

Vitis. In the grape, Vitis (garden varieties), the cotyledons are opposite, ovate, entire. The nepionic leaves are cordate, slightly trilobed. In later growth, leaves become more lobate, and tendrils, which are absent in the young, begin to appear. In adult vines the young leaves, when they first appear, are strikingly like the seedling, not taking on the full lobate character until later growth. Nepionic leaves and young leaves of new growths resemble fossil species of Vitis in their trilobed form and general simplicity of outline.

Ampelopsis quinquefolia. In the Virginia Creeper (*Ampelopsis quinquefolia* Mich.) the seedling (Pl. 16, fig. 19) has ovate cotyledons resembling those of *A. tricuspidata*. The first two succeeding nepionic leaves are trifoliolate, alternate, as in *A. tricuspidata*, but they differ from that species somewhat in form; compare Fig. 19, and Pl. 17, fig. 20. The third leaf has attained adult characters. The adult has compound leaves of five leaflets, not unifoliolate leaves, as in *A. tricuspidata*. The adult does not present localized stages, excepting that occasional leaves are reversionary in being trifoliolate. These leaves may be borne on any part of the plant, and occasional branches bear many such leaves. This is especially seen in late terminal branches.

Ampelopsis tricuspidata. The Japanese Ivy, *Ampelopsis tricuspidata* Sieb. and Zucc. (*A. veitchii* Hort.), which is extensively cultivated as an ornamental vine, presents striking features. In the seedling (Pl. 17, fig. 20) the cotyledons are broadly ovate, entire. The nepionic leaves are trifoliolate and alternate. The individual leaflets of these nepionic leaves are irregularly ovate and dentate. It is noticeable that lateral leaflets conform in outline to the shape of the terminal leaflet, and also that dentations are absent in those portions of the leaflets which lie adjacent to one another, as in *A. quinquefolia*. This trifoliolate stage is retained for a considerable period, through the first year's growth in the specimens observed. In seedlings of the second year's growth, trifoliolate leaves occur on the proximal part; but beyond them the leaves (Pl. 17, fig. 21) are unifoliolate. subcordate, deeply denticulate. This form of leaf is retained throughout the second year.

In adult *Ampelopsis tricuspidata* localized stages in development are very marked. At the base of the vine, and to a distance of three or four feet from the root, all the leaves are trifoliolate (Pl. 17, figs. 23, 25), repeating in form the nepionic leaves of the seedling (Pl. 17, fig. 20). No trilobed or cordate unifoliolate leaves are found at this area in vines raised from seed. In vines raised from cuttings, as is frequently done, the leaves at this area do not have the trifoliolate character, but are unifoliolate and trilobed. I am informed by a nurseryman that he adopts the method of propagating by cuttings to gain uniformity in the leaves of the vine. The occurrence of typical nepionic leaves at this area is in entire accord with what is shown in regard to suckers from the base in many plants; namely, that at the nepionic area there is a tendency to produce nepionic leaves throughout the life of the individual. Beyond the trifoliolate leaves at the base, all the leaves on the old wood (preceding the current season's growth) are unifoliolate and trilobed (Pl. 17, figs. 22, 25), this being the "character" leaf of the species. In an adult in the current season's growth, still a third type of leaf is found. This is cordate, deeply toothed (Pl. 17, figs. 24, 25), and repeats the form which is characteristic of the second nepionic stage of the seedling (Pl. 17, fig. 21). The leaves of the adult in this species, which at first sight appear to be simple, should be considered compound leaves, reduced to a single leaflet. The truth of this is evinced by the fact, that, when the leaves drop in the autumn, an articulation develops, and the leaves separate from the petiole at the proximal border of the blade. The petiole may remain in place for a considerable time after the fall of the single leaflet. The trifoliolate leaves at the base of the vine separate from the petiole in a similar manner, but leave three scars at the distal end of the petiole instead of a single one.

Ampelopsis tricuspidata may fairly be considered a regressive species, in which the unifoliolate character is developed by dropping out the two lateral leaflets from the proximal portion of the leaf. In the adult, when the leaves come out in spring, those at the base of the vine are all trifoliolate (Pl. 17, fig. 25. area a); those on the old wood are unifoliolate, trilobed (the same figure, area b); and those on the new growth are cordate dentate (same figure, area c). There are thus to be seen three zones or localized stages: a, which repeats nepionic characters; b, which has attained full specific characters; and c, which repeats the second nepionic stage of the young. Plants vary so much in the form of their leaves that *Ampelopsis tricuspidata* is noteworthy on account of the constancy of the form of its leaves. At the base of plants raised from seed the leaves are always trifoliolate; when unifoliolate trilobed leaves appear, they mark a sharp line of distinction, and very rarely do more trifoliolate leaves occur; cordate leaves are found only on branches of the current season's growth. In the diagram (Pl. 17, fig. 25), the current season's growth is represented as area c, or on the periphery. Of course in practice new branches may start out from any part of the plant, but wherever they originate, they are marked by the same type of leaves. When new branches originate from the base within the trifoliolate leaf area a, then cordate leaves immediately succeed trifoliolate leaves, as in seedlings.

ACER RUBRUM. The seedling Red Maple, *Acer rubrum* L. (Pl. 17, fig. 28), has two long, strap-shaped cotyledons, rounded distally. The first nepionic leaves are opposite, elongate, cordate, acuminate, dentate. They already show indications of the trilobed character of the species in the slightly larger lateral lobes near the base of the leaf. The second pair of leaves is elongate, but differs from the first in the greater development of the two lateral lobes, rendering the leaf trilobate; but the median lobe is markedly elongate. The same features, though in slightly varying degrees, are characteristic of seedlings of *Acer saccharum* Marsh, *A. spicatum* L., *A. platanoides* L., and *A. pseudoplatanus* L. In *Acer pennsylvanicum* L., the first pair of nepionic leaves is simpler than in the species noted, being ovate, dentate, with no evidence of a trilobed character as described by Mr. Deane ('96). This species in its development is structurally the most primitive species of maple seen.

As the Red Maple grows older, the trilobate character becomes more marked, and two additional lateral lobes may appear on the proximal border of the leaves. The feature of change is the relative shortening of the median and enlargement of the lateral lobes. The leaf of the adult tree is trilobed or slightly five-lobed (Pl. 17, fig. 29, leaf 1). Individual trees with trilobed leaves may properly be considered more primitive in character than those with five-lobed leaves, as they bear a closer resemblance to the young and fossil forms; also they are less differentiated on the proximal portion.

In the Red Maple, young suckers from the base (Pl. 17, fig. 27), or other part of the tree, have trilobed leaves in which the median lobe is elongate, as in the seedling. In vigorous shoots, or young leaves at the tips of branches (Pl. 17, figs. 26, 29), or in the axils of older leaves, the leaves are also trilobed, with an elongate, median lobe, as in the seedling. In *Acer spicatum* Mr. Deane ('96) observes that, "The leaves on the ends of new shoots in the old plants resemble in shape and size the first leaves of the seedling." This and many other facts are shown in Mr. Deane's very interesting collection of seedlings. Elongate weakly trilobed leaves on terminal shoots, similar to the seedling, also occur in the White Maple (*Acer saccharinum* L.), Moose-wood (*Acer pennsylvanicum*), and Norway Maple (*Acer platanoides*). In the Moose-wood the leaves may even be entire, as noted in the young seedling of that species.

ACER PLATANOIDES. In *Acer platanoides* the leaves are palmately five-lobed, but seedlings closely resemble the seedlings of the Red Maple. Suckers from a stump of this species (Pl. 18, fig. 34) at the base, had trilobed leaves with an elongate median lobe, as in the young. The succeeding leaves, however, were palmately five-lobed, nearly or quite as in the adult. Similar trilobed leaves occur in suckers at the base of the White Maple (*Acer saccharinum*).

CHINESE AND JAPANESE MAPLES. In China and Japan there is a very interesting series of primitive types of maples, for the opportunity of studying which I am indebted to the Arnold arboretum.

Acer oblongum Wall., from the Province of Hu-Peh, China, Coll. Dr. Aug. Henry. In this species the leaves (Pl. 17, fig. 30) are elongate, oval, acuminate, margins entire. It would hardly, if at all, be recognized as belonging to this genus, were it not for the fruit. Besides the median vein, two strong lateral veins diverge from the base, as is usual in maples. All the evidence of palaeontology and ontogeny shows that entire leaves are more primitive than dentate or lobed leaves. Therefore we may properly consider this as an extremely primitive type, in fact structurally more primitive than any other known living or fossil species of maple. It is also more primitive structurally than the known seedling maples.

Acer carpinifolium S. and Z., from Nikko, Japan, Coll. Prof. C. S. Sargent, is another very striking type. The leaves (Pl. 17, fig. 31) are elongate, oval, acuminate, with serrate margins. The leaves at the end of the branch have slight marginal undulations about 15 mm. from the base, as in the figure. Leaves situated nearer the base of the branch do not show these undulations, but are slightly inequilateral. The veins are given off obliquely from the midrib and are parallel to one another, no strongly marked lateral veins existing, as in *Acer oblongum*. This species may be considered as structurally more specialized than *Acer oblongum* on account of its dentate margins.

Acer crataegifolium S. and Z., from Nikko, Japan, Coll. Prof. C. S. Sargent, is an interesting type. The leaves (Pl. 17, fig. 32) are broadly oval and slightly dentate, two of the serrations on the sides being strongly marked, so that the leaf strikingly resembles the first nepionic leaves of the seedling of the Red Maple (Fig. 28, leaf 1). It is also quite like the simplest of the fossil maples, as *Acer indivisum* Web., of the late Cretaceous (Laramie) and Tertiary. All the leaves of this species are similar, no variation having been observed. It is a distinctly archaic type in its form.

Acer tartaricum L. var. *ginnale* Maxim., from Jesso, Japan. Coll. Dr. H. Mayr, presents interesting features. On the proximal end of the branchlets (Pl. 17, fig. 33) are two bluntly oval, very slightly serrate leaves; similar leaves occur on many specimens seen in the herbarium of the Arnold arboretum. Beyond this single pair of leaves all the leaves are of a strikingly different form (Fig. 33); they are elongate, slightly trilobed, with serrate margins. Individual leaves show considerable variation in the trilobed character, some being less, others a little more, deeply trilobed than the leaves figured, which represent a fair average. This type of leaf bears considerable resemblance to the weakly trilobed leaves seen in the second pair of leaves and in the later leaves of young Red Maples (Fig. 28) and other species. It may, therefore, in the character of these leaves be considered a primitive type but more advanced structurally than *Acer crataegifolium*. In regard to the two oval nearly entire leaves seen at the base (Pl. 17, fig. 33), they may be considered a localized reversion to a simpler type, and as such may be compared to *Gleditschia triacanthos* in which the proximal leaves are once compound, the distal being more specialized and twice compound. (See p. 102.)

Fossil Maples. In *Acer indivisum* Web., of the late Cretaceous and Tertiary, we find a type in which the leaves are either without lobes, or with two slight lobes quite similar to the first nepionic leaves of *Acer rubrum* and *A. pseudo-platanus*. In the Cretaceous and Tertiary maples the species are almost universally trilobed, and an elongate character of the median lobe is of frequent occurrence, as in *Acer trilobatum* A. Br. and *A. decipiens* Heer. The trilobed character of maples finds, then, an expression in many fossil species and primitive living species, as *Acer crataegifolium* and *A. rubrum*. An elongate trilobed form is seen in some fossil species, in the young of all species observed, and in vigorous growths, and leaves of terminal branches of *Acer rubrum* and many other species. *Acer pennsylvanicum* forms a partial exception to this rule, because the first pair of nepionic leaves shows no trilobate character, this feature being developed in later growth. Species such as the Sugar, White, and Norway Maples, besides other features are differentiated by having two lobes added to the proximal end of the leaf, but in the young and degradational leaves they show the more primitive trilobed character.

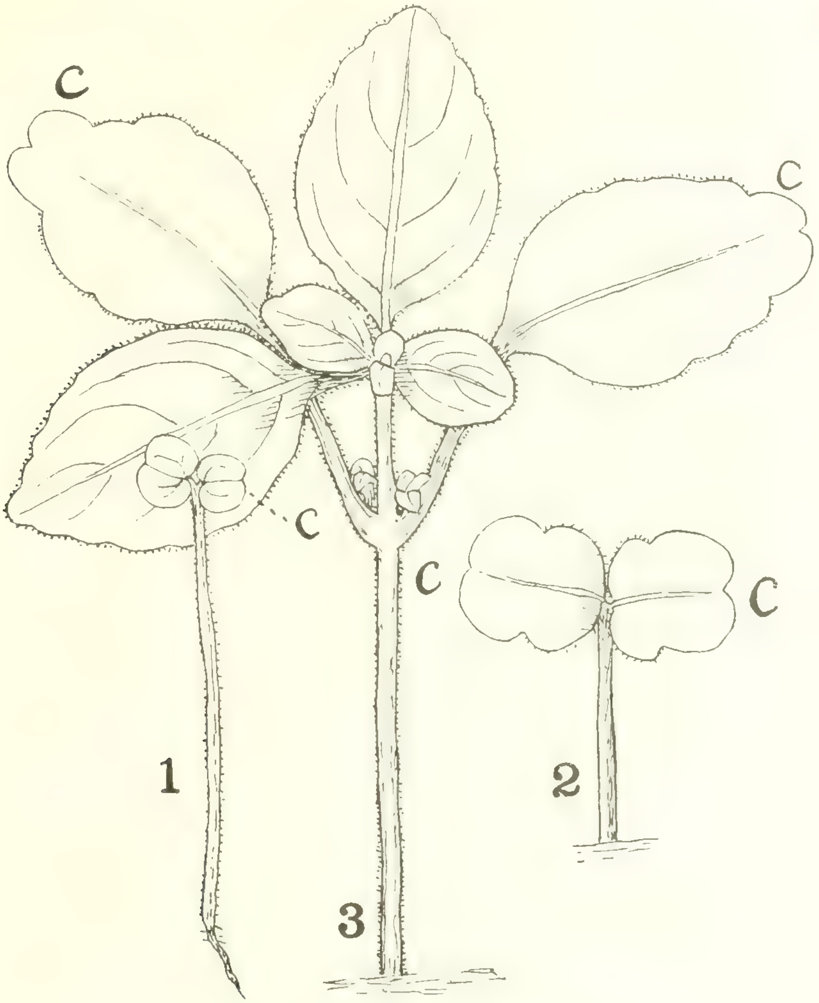
Negundo aceroides. In the Ash-leaved Maple, *Negundo aceroides* M., the seedling has simple trilobed leaves. My material is imperfect, and first nepionic leaves and cotyledons are not shown on the specimens. In later growth the leaves are trifoliolate. In the adult the leaves are very variable in outline and degree of division, having from three to seven leaflets. Occasional simple leaves are also seen as reversions. The terminal and lateral leaflets vary much in outline (Pl. 18, fig. 36), being ovate, denticulate, trilobed, or even twice pinnate. When trilobed, as in the terminal leaflet of the figure, they bear considerable resemblance to the nepionic leaves of the seedling. A sucker from the base of an adult (Pl. 18, fig. 35) has first a simple trilobed leaf, like the young, also like the simpler fossil and living species of maples. The second leaf of this sucker is trifoliolate. In two other suckers, two simple trilobed leaves precede the first compound leaves. The seedlings, suckers, and often the terminal leaflets, therefore, show distinctly reversionary characters.

GYMNOCLADUS DISICUS. In the Kentucky Coffee-tree (*Gymnocladus disicus* L.) the leaves (Pl. 18, fig. 37) are very large and twice paripinnate. The proximal end of the leaf, however, has two, three, or four simple leaflets, commonly four. The total number of leaflets on large leaves counted varied from seventy-five to one hundred and seventeen. I have not seen seedlings of this species, but it suckers freely from underground roots. The sucker (Pl. 18, fig. 38) has once compound leaves, composed of few leaflets, four in the specimen figured, which was the smallest number seen. Later leaves on the sucker rapidly increase in the number of leaflets and soon become twice compound. From evidence in other types, it is probable that the nepionic leaves of the seedling are very similar to the first leaves of the sucker. In many cases, as noted, the distal portion of the leaf repeats the form of nepionic leaves. It is interesting to note that here the proximal portion of the adult leaf resembles the once pinnate condition of the leaf of the sucker and presumably of the seedling; in so far it is reversionary in character.

GLEDITSCHIA TRIACANTHOS. In the Honey Locust (*Gleditschia triacanthos* L.) the seedling has thick, fleshy, rounded cotyledons (Pl. 18, fig. 39). They are auricled at the base, nearly embracing the stem, as shown in Fig. 39a. The nepionic leaves are alternate, once compound, paripinnate. The first leaf has numerous leaflets, sessile, not quite opposite one another. Succeeding leaves are similar, but progressively larger, with more leaflets. The leaves of the adult are once or twice paripinnate. The twice pinnate leaves are borne on the new growth at the ends of the branches; but the leaves of the old wood or proximal portion of the branches are once pinnate. The old wood, therefore, bears the more primitive, the new wood the more specialized type of leaf. Occasionally a few once compound leaves are seen on the new wood as a reversionary variation. The distal end of once pinnate leaves or the end of the second division of twice compound leaves repeats the form of the nepionic leaves of the seedling. It is noted in many cases that the distal end of adult simple or compound imparipinnate leaves closely resembles the form of the first nepionic leaves of the seedling. Such seems to be the case usually in paripinnate leaves as well. Besides the cases noted numerous confirmatory cases may be seen by looking over Lubbock's book ('92) on seedlings. In plants where later leaves are radically different from the seedling, as in many acacias, cactuses, etc., of course this parallelism would not hold true. At least occasional exceptions occur, however, as in *Sesbania tomentosa* Hook. and Arn., figured by Lubbock ('92). In this type the first nepionic leaf is simple, but later leaves are paripinnate.

In twice compound leaves of the Honey Locust frequently a single leaflet takes the place of a compound leaflet, evincing a reversionary character.

Eucharidium grandiflorum. The seedling of *Eucharidium grandiflorum* Fisch. and Mey., as described by Lubbock ('92), presents a graphic case of the change in the form



Eucharidium grandiflorum.

1. Seedling, × 3. 2. The same, ten days after germination, × 3.
3. The same, showing final form of cotyledons and succeeding nepionic leaves, × 1. c, cotyledon.

of leaves during growth. This is reproduced here by the courtesy of Messrs. D. Appleton and Company. Lubbock shows that in the seedling the cotyledons are first sessile, oblong-orbicular, auricled at the base, and with an emarginate tip (Fig. 1). In later growth a slight constriction appears near the base on either side. "This basal portion increases much more rapidly, while the growth of the terminal portion (which is, in fact, the original cotyledon) becomes gradually arrested." (Fig. 2.) "In its final form (fig. [3]) the new portion is both broader and longer than the true cotyledon, and differs from it not only in the crenations, but in the possession of a more conspicuous midrib and rather stiff hairs. Not only is this basal portion interesting in its mode of development, but also from its similarity to the subsequent leaves. In fact, * * * it may be said that we have a compound structure formed of a leaf at the base, terminated by the cotyledon." He describes similar changes in cotyledons of species of Clarkia and Oenothera. These cases are very interesting as cases of accelerated development, in which features ordinarily originating later are shoved back into embryonic stages. They are especially interesting to us here, however, as illustrating localized stages in development in the ontogenesis of a leaf, showing that in progressive periods of its growth it may actually acquire features which make the characters of the leaf an epitome of the development of the type. Special attention is called to the fact, that the new additions are made to the proximal portion of the leaf, the distal portion retaining its original characters.

FATSIA JAPONICA. The seedling of *Fatsia japonica* Decne and Planch. (*Aralia sieboldii* Hort.) (Pl. 18, fig. 41) has obovate rounded cotyledons. Succeeding nepionic leaves are alternate, the first leaf is broadly ovate, the second cordate, both finely dentate, and the third leaf is trilobed. The first two leaves closely resemble the leaves of the same stage in *Aralia edulis* Sieb. and Zucc., as figured by Lubbock ('92). The adult leaves of that species are large and bipinnate. In adult *Fatsia japonica* the leaves are large, palmately deeply cleft, serrate (Pl. 18, fig. 40). In two plants some six feet high (raised from seed), which were cut down nearly to the ground, suckers were thrown out. In the sucker (Pl. 18, fig. 42), the first two leaves are in one case broadly cordate, dentate, in the other trilobed, both resembling closely the nepionic leaves of the seedling. It should be noted, however, that in the sucker the first leaf is trilobed, the second cordate, whereas the reverse order is the condition of the seedling. *Aralia notata* Lx. of the Cretaceous is trilobed and closely resembles the trilobed leaf of the seedling and sucker of *Fatsia japonica*.

HEDERA HELIX. In the English Ivy (*Hedera helix* L.), the seedling (Pl. 18, fig. 43) has two broadly ovate cotyledons. Succeeding nepionic leaves are alternate. The first nepionic leaf is broadly ovate, with only a slight indication of a lobe on one side. The second leaf is also broadly ovate, and has a slightly developed lobe on either side. The third leaf is a "character" leaf, having nearly or quite the full characters of the species. It is five-lobed, whereas in some other seedlings the third leaf is trilobed; but this is perhaps no more than might be expected in this protean species. The fourth leaf is also five-lobed, but the lobation is not so pronounced as in the third. The fifth leaf, which is very young, is slightly trilobed, resembling the second nepionic leaf. It is reasonable to suppose that in further growth this young leaf would have taken on additional lobes like the third and fourth nepionic leaves. For this and many other seedlings I am indebted to Mrs. Robert T. Jackson.

The English Ivy varies greatly, but selecting a branch, the fully grown leaf of which is like the seedling figured, a comparison may be made. In such a branch (Pl. 18, fig. 44), the fully developed leaf is five-lobed. Passing upward to the youngest leaves at the tip of the branch, we find that the lobes become progressively reduced. The fifth leaf has five lobes, but not strongly developed; the sixth and seventh are simply trilobed. The eighth leaf is weakly trilobed, and bears considerable resemblance to the second nepionic leaf of the seedling. While the leaves are very variable, it may be said that the young leaves of new growths have fewer lobes or at least more weakly developed lobes than the older leaves on the branches, thus making a more or less complete reversion to the simple condition of the young. It is noteworthy that the simple trilobed leaves of young seedlings and young leaves at the end of growing shoots (Pl. 18, figs. 43, 44) bear a close resemblance to *Hedera cretacea* Lesq., of the Cretaceous.

DAHLIA VARIABILIS. The seedling of the common Dahlia (*D. variabilis* Desf.), has simple, ovate leaves, succeeded by pinnatisect leaves. The typical leaves of the adult have three, or more often five segments. Suckers from the crown frequently have simple, ovate leaves at first, as in the seedling. On flowering shoots, especially late in autumn, simple leaves are so common as almost to predominate. In these simple leaves are seen distinct localized reversions to the simple condition characteristic of the young.

TECOMA RADICANS. In the Trumpet Vine (*Tecoma radicans* Juss.) the seedling has rounded cotyledons, distally deeply notched. The first nepionic leaves are simple, dentate, with petioles. There are two pairs of simple leaves, succeeded by compound, trifoliolate leaves. In later stages, additional leaflets appear, until the full character leaves are attained. The distal leaflet of adult leaves resembles the simple nepionic leaf. In suckers from the root, cases occur in which the first leaves are simple, as in the seedling. Often, however, the first leaves developed in suckers are trifoliolate, the reversion being more or less complete in different individuals.

FRAXINUS AMERICANA. The ashes present interesting features in development and localized stages in development. In the development of the White Ash (*Fraxinus americana* L.) the seedling (Pl. 18, fig. 45) has oblong, obtuse cotyledons. The nepionic leaves are opposite, simple, oval, with acuminate tips and long petioles. Several alternating pairs (five or six) of simple opposite leaves appear, all having the same outline, excepting that occasional abnormal leaves are blunter distally or even rounded and distally emarginate. These variations in the cases noted usually occur in both leaves of the pair. The first compound leaves, as shown in an older seedling (Pl. 18, fig. 46), are trifoliolate, the distal leaflet resembling the earlier simple leaves; the lateral leaflets are similar but sessile. Gradually later added leaves become more differentiated by the addition of lateral leaflets proximally, until there are from seven to nine leaflets, which are characteristic of the species. During later growth, petiolules develop on the lateral leaflets, until they are comparatively long, as in the adult (Pl. 18, fig. 48).

In the adult White Ash the leaves (Pl. 18, fig. 48) are large, and the terminal leaflet closely resembles the simple nepionic leaves of the seedling. The White Ash suckers quite freely from roots near the base of the tree or from the stump when a tree has been cut down. Such suckers repeat very closely the form of seedlings. One of a number of suckers from the base of a tree some forty feet high is represented in Pl. 18, fig. 47. The first leaves are simple and alternate, as is frequent in suckers of the ash, although they are often opposite, as in seedlings. The first simple leaves also are often rounded distally instead of acuminate as in seedlings. These and other variations are more frequent in suckers from large trees than from small ones. After more or less simple leaves, usually several, the compound leaves appear. The first compound leaves are usually trifoliolate as in seedlings, in later leaves lateral leaflets are progressively added proximally, as in the growing seedling, also lateral leaflets are sessile as in seedlings. The last of the simple leaves and the compound leaves (Pl. 18, fig. 47) are quite strongly serrate, a feature which is less marked or absent in seedlings. In suckers from stumps of large trees that have been cut down, the first leaves are often compound, being trifoliolate or even five-foliate; nevertheless suckers with simple leaves at their base may be considered the typical form. The only important differences noted between typical suckers and seedlings are that leaves are very commonly alternate in suckers and that they undergo frequently an accelerated development, acquiring adult characters earlier than seedlings. To this may be added considerable variability in the outline of leaves in suckers.

In growths thrown out late in the season from any part of the tree, it is noticeable that the lateral leaflets are frequently sessile, in this resembling the character of nepionic leaves. In the adult White Ash occasionally leaves of three or five leaflets, or rarely simple leaves, are found instead of the typical number. Such primitive leaves may fairly be considered as cases of arrested development, in which during the ontogenesis of the leaf the later added characters were skipped. It is to be noted, as observed in many other cases, that it is the proximal, or last added, portion which is repressed.

FRAXINUS ANOMALA. According to Professor Sargent ('91-'97) *Fraxinus anomala* Wats. is a small tree or shrub which usually bears simple leaves, but occasionally leaves which are trifoliolate or five-foliate. Such compound leaves are doubtless reversions, and appear to be comparable to the reversionary leaves just mentioned in the White Ash. One is a case of failure to develop the full specific characters in a progressive type, as the other is a case of developing more than the full specific characters in a regressive type; but both are localized ontogenies of a reversionary character. In Mr. Faxon's drawing *Fraxinus anomala*, in Professor Sargent's Silva, the typical single leaves are rounded, with long petioles, resembling the rounded leaves seen often in seedlings or suckers of the White Ash. The terminal leaflets of compound leaves, and simple leaves on flowering branches, are acuminate as in other ashes. The development of *Fraxinus anomala* should be interesting.

FRAXINUS PUBESCENS. The seedling of the Red Ash (*Fraxinus pubescens* Lam.) closely resembles that of the White Ash. The cotyledons are similar, and there are five or six pairs of simple leaves which are oval, elongate. They differ, however, from the similar leaves of the White Ash in being less acuminate distally, deeper green, and the later simple leaves are finely serrate. While serrations occur on all my specimens, they were from one locality, and other seedlings might not be serrate, as adults vary in this character. The compound leaves appear, as in the White Ash, first as trifoliolate leaves, later with more divided leaves. Leaves formed late in the season's growth, in the Red Ash, show a tendency toward sessile lateral leaflets, as in the White Ash.

OTHER ASHES. According to Sir John Lubbock, the seedling of *Fraxinus excelsior* L. has but one pair of simple nepionic leaves, the second pair being trifoliolate. Both sets are serrate. This species is markedly accelerated in its development, as compared with the Red and White Ash, on account of acquiring compound leaves so much earlier.

We find that the seedlings of the Red Ash and the White Ash have simple leaves, followed by compound leaves, the lateral leaflets of which are sessile. These features are repeated in suckers of the White Ash. The distal leaflet of adult leaves of both species resembles the simple nepionic leaves, and leaves of late growths tend to reduce the petiolules in lateral leaflets, as in the young. In the Black Ash (*Fraxinus sambucifolia* Lam.) the primitive character of sessile lateral leaflets is characteristic of the adult, but the distal leaflet has a long petiolule as in other species. The same characters exist in the European Ash (*Fraxinus excelsior* L.), *Fraxinus australis* Gay, and usually in *F. oregona* Nutt. In fossil ashes the lateral leaflets are sessile, as in the young of specialized and adult of what in this feature, at least, are primitive species.

SASSAFRAS SASSAFRAS. In *Sassafras sassafras* Karsten (*S. officinale* Nees) the seedling (Pl. 19, fig. 49) retains the fruit in place and leafy cotyledons are not developed. The nepionic leaves are arranged alternately on the stem. The first nepionic leaves are small, ovally rounded; later leaves retain the same oval outline but increase greatly in size. In the specimen figured the sixth leaf from the base shows slight marginal undulations, which may be the first appearance of lobes; but such do not often occur until considerably later. In Pl. 19, fig. 50, is shown the upper part of an older seedling. The lower part of this specimen had only oval leaves, as in Fig. 49, but the upper part bears three leaves with two or three lobes. In seedlings the lobed leaves occur in the upper part or later growth only; but in this same area some ovate leaves are not infrequently associated with the lobed leaves. In the adult tree the leaves are borne on short branchlets of the current season's growth. At the base or proximal portion of such branches (Pl. 19, fig. 51), all the leaves are ovally rounded, ovate or obovate, as in the young seedling. At the upper part of the branch, however, lobed leaves are often developed, although many branches bear no lobed leaves. Amongst the lobed leaves of the upper part of the branch, ovate leaves may or may not develop, this feature being variable. Each branch of the adult, therefore, which bears lobed leaves, repeats the features characteristic of the seedling, having oval leaves proximally and leaves with two or three lobes distally, with or without associated oval leaves. Lobed leaves are much more common in plants up to five or six feet high than in adults. As branches of adults bear oval leaves throughout the branch or on the proximal part, when distal leaves are lobed, therefore oval leaves are the dominant type, the lobed leaves the exceptional. Professor Ward ('88) maintains the same view. The Sassafras suckers freely from the root, and such suckers repeat the form of the seedling so closely that often they cannot be distinguished until the root is examined.

The Sassafras is abundantly represented in the Dakota group (Cretaceous) of this country. These old species (Lesquereux, '91) are two- or three-lobed, similarly to the lobed condition of modern *Sassafras sassafras* in the later growths of seedlings or occasional leaves at the tips of branches of adults. The fact that seedlings start with entire leaves and later acquire lobed leaves like the earliest fossil representatives seems difficult to harmonize with the usual condition, where the first leaves are like the primitive or ancient types, and later leaves are different, being more specialized, as in Liriodendron, White Ash, and Platanus. They may be less specialized, however, as in *Ampelopsis tricuspidata* and *Fraxinus anomala*. Granting that in adult *Sassafras sassafras* the oval leaves are by far the most numerous, also that lobed leaves when existent are pretty definitely limited to a certain portion of the branch, the end, we may fairly assume that the lobed leaves are not the typical leaf of the species, but are localized reversions of frequent occurrence. By the principle of acceleration of development stages are shoved back earlier and earlier, so that we expect to find ancestral stages in the very young. In this species, however, the species features (oval leaves) are found in the young seedling (Pl. 19, fig. 49), and ancestral features (lobed leaves) do not come until late in the growth of the seedling (Pl. 19, fig. 50). As shown by Cope, types may lose ancestral characters by retardation of development. That is, features may appear at later and later stages in development until they finally disappear. A common case is the late appearance or entire want of the last molar or wisdom teeth in man. To apply this principle to the Sassafras: if we assume that it is a reversionary type, repeating more or less fully the characters of types earlier than the known Cretaceous lobed forms, then by the principle of retardation the lobed features (Cretaceous) would appear later and later in the ontogeny (seedling) and be present in latest growths of the adult (tips of branches), or absent, as is the case. While this view is open to doubt, it is in accordance with the facts and seems worth consideration. Associated genera, as Laurus, Persea, and Cinnamomum, are characterized by leaves which are simple in outline both in fossil and living species.

PLATANUS OCCIDENTALIS. In *Platanus orientalis* L., according to Lubbock ('92), the seedling (Pl. 19, fig. 54) has cotyledons which are narrow, spathulate, tapering to the base. The nepionic leaves are alternate, spathulate, cuneate, distally bluntly tridentate. I have not seen seedlings of our species, *Platanus occidentalis* L.; but we may assume that it is similar to the same stage of the nearly allied European form. Suckers from the base of an adult tree (Pl. 19, figs. 55, 56) have leaves which are quite similar to nepionic leaves of the seedling. The first leaves (Fig. 55) are elongate spathulate, distally dentate, laterally nearly or quite entire. While the tips are variable in outline they are frequently tridentate as in leaf 1, Fig. 56, and some such leaves occur on all suckers. Leaves at the base of the sucker (leaf 1) are more elongate and spathulate than later leaves, thus making a closer approach to the character of the seedling. A noticeable feature is the fact that the blade of the leaf extends down on the petiole, forming an acute angle basally, as in seedlings and many fossil species. The trilobed leaves of the sucker, as leaves 2 and 3, Fig. 56, closely resemble fossil species of Platanus, as *P. primaera* Lesq. from the Cretaceous (Dakota group). At the height of several feet from the ground suckers usually develop very large strongly five-lobed leaves numerously and deeply dentate (Pl. 19, fig. 58). The most striking feature, however, is the development of the base of the blade into a lobed basal appendage which is more or less extensively developed. Nerves run upon this appendage from the point of disappearance of the main veins of the leaf proper, as shown in the figure. On the lower side of the leaf it is seen (Fig. 58a) that this appendage stands out free from the petiole so that the leaf is perfoliate. At the base of the petiole in the case of these vigorous leaves the branch is enveloped by an extravagant development of the stipules (Fig. 58b), which fuse and form an encircling ruffle. These characters are seen frequently also on vigorous leaves of adults especially those growing in wet bottom lands; but they are quite distinct from the characters of the typical leaves of the species. After making the above drawings and observations I was much interested to find that Prof. Lester F. Ward ('88) had made similar observations, and he compares this lobate condition of modern Platanus with a similar basal lobate appendage in *Platanus basilobata* Ward, of the Laramie group (Cretaceous). There is a difference, however, as *P. basilobata* has much larger basal lobes and the upper part of the leaf is trilobate instead of five-lobed. In the Cretaceous *Aspidiophyllum dentatum* Lesq. a similar strongly marked basal appendage occurs. Ward ('88) and Lesquereux ('91) note this striking similarity to leaves seen in living Platanus as described, and further the fact that the nervation of *A. dentatum* is very similar to that of Platanus. All the evidence would seem to show that the Cretaceous Aspidiophyllum is an ancient though somewhat aberrant form of Platanus. It is quite possible that the extravagant development of basal appendages in these several types represents parallel differentiation in related forms rather than direct phylogenetic association.

The typical leaves of adult *Platanus occidentalis* (Pl. 19, fig. 57) are broadly pentagonal, five-lobed, dentate, the base of the leaf extending down slightly on the stem forming an obtuse angle proximally instead of an acute angle as in seedlings, young suckers, and many fossil forms. This basal portion is adnate to the petiole and the midrib extends to its base. As variations, leaves are frequently found which have none of the secondary dentations, as in the specimen figured; also the two proximal lobes are frequently wanting, and the leaf becomes trilobate and resembles more or less closely leaf 3 of Fig. 56 and fossil allies as *Platanus primaeva* Lesq., of the Cretaceous.

HICORIA OVATA. In the Shag-bark, *Hicoria ovata* (Mill.) Britton, in normal germination the nut rests on the surface of the ground (Pl. 20, fig. 59). The first leaves are simple, oval, slightly serrate, with the apex pointed bluntly. The specimen figured has lost the leaves at the lower portion of the stem, but I did not succeed in finding a specimen with these in place. The fourth leaf is distorted and besides the distal leaflet has a small lateral leaflet on one side. The fifth and sixth leaves are trifoliolate. The distal leaflets of these compound leaves are practically like the first simple leaf, but lateral leaflets are shorter and smaller.

In the adult of this species the leaves are compound, composed of five leaflets (Pl. 20, fig. 61, leaf 1), and the distal leaflet bears a considerable resemblance to the first simple nepionic leaves of the seedling. At the tips of branches of adults there is characteristically one (sometimes two or three), trifoliolate leaves (Pl. 20, fig. 61, leaf 2). Such trifoliolate leaves are not borne normally on any other part of the branch and represent a localized reversion, comparable to the later stages in development of the leaves of the seedling (Fig. 59).

The Shag-bark does not sucker freely; but a sucker from the root of an adult (Pl. 20, fig. 60) shows interesting features. The first three leaves are wanting, the fourth and fifth are simple, resembling the simple leaves of the seedling, except in size and the fact that the fifth leaf is very broad basally. The sixth and seventh leaves are abnormal (a common feature in suckers), being very large, irregular in outline, and each having one lateral leaflet. The ninth and tenth leaves are trifoliolate and near enough to be comparable to trifoliolate leaves of the seedling. In the Shag-bark, therefore, we find a repetition of nepionic characters in suckers and partially in the trifoliolate terminal leaves of branches.

Trifoliolate leaves at the tips of the branches of adults as in the Shag-bark have also been observed as characteristic of the Pig-nut, *Hicoria glabra* (Mill.) Britton, and the Mockernut, *Hicoria alba* (L.) Britton.

QUERCUS ALBA. In the White Oak (*Quercus alba* L.), the seedling (Pl. 20, fig. 62) has a long, stout, flexuous root. The cotyledons remain in the acorn, buried just beneath the surface of the soil. The stem is bare for a considerable distance, the first leaves not developing, but axillary buds are prominent, as represented in the figure. The first leaf is ovally rounded, slightly sinuous; in seedlings this leaf is sometimes more or less sinuous than in the first leaf of the specimen figured. The second and third leaves of the specimen figured are gently lobed, and succeeding leaves in older specimens rapidly take on a more deeply lobed character, until they make some approach to the form of the leaves of the adult (Pl. 20, fig. 64). These early leaves are smooth, and deep green, as in the adult. In suckers from the base of the White Oak the first formed leaves are more or less ovate and slightly sinuous in outline (Pl. 20, fig. 63). They are variable, but the sucker figured represents a fair average specimen. Later formed leaves rapidly take on mature characters, as indicated by the lobation of the third leaf in the sucker figured. In the adult, on weak shoots, leaves are frequently seen which are simple in outline as in the sucker and seedling, indicating localized reversionary characters.

QUERCUS MINOR. Of the Post Oak (*Quercus minor* (Marsh) Sarg.) I have not seen seedlings, but suckers from the base of adults have ovate or obovate leaves with gently wavy margins as in the specimen figured (Pl. 20, fig 65). These early leaves have the deep green, roughness, and leathery texture of adult leaves. During further growth the later added leaves rapidly assume the lobed form of leaves of the species, which is very marked in character (Pl. 20, fig. 66).

QUERCUS TINCTORIA. The Black Oak (*Quercus tinctoria* Bar.) and Scarlet Oak (*Quercus coccinea* Wang.) both occurred in the woods where the seedlings described were collected. As these species are so close, the seedlings with present knowledge cannot under the circumstances be certainly referred to either species. The seedlings (Pl. 20, figs. 67 and 68) have stout, flexuous roots, but not quite so markedly as in the White

Oak (Fig. 62). The cotyledons remain in the acorn beneath the surface as in the White Oak and some other, perhaps all, species of the genus. The petioles of the cotyledons extend beyond the acorn, embracing the stem, as shown in the seedlings figured. In Fig. 67 the thick, rounded cotyledons are shown with the acorn husk removed. The first few leaves are reduced to scales, axillary buds being the most prominent feature. The first leaves developed (Pl. 20, figs. 67, 68) vary in size, are ovally rounded, and bear a minute tooth at the end of the median rib, but are otherwise entire. While the specimens figured represent typical individuals, sometimes the first leaves have minute teeth at the end of a few lateral veins as well as the median vein; in such specimens the leaf may or may not have a slightly flexuous margin. In Fig. 67, the first three leaves have only a slight tooth at the distal end, the fourth leaf has a slightly sinuous margin, and minute teeth at the tips of principal veins. In Fig. 68, the first two leaves are entire and smaller than the average. The next two leaves have sinuous margins and teeth at the ends of principal veins. In later growth the leaves become more deeply lobed with pronounced bristles. The leaves of these young oaks are rather bright green, lusterless, covered with fine hairs arranged in a stellate manner. If the growth of the first year dies, a new growth springs up from the base, which is indistinguishable from an actual seedling, and this may happen several times. I have frequently dug up such relatively old plants for seedlings and not found the mistake until the scars of previous growths were seen. That is, at this localized area nepionic leaves are produced continually, as in many other plants, although the plant may actually be several years old.

Suckers from the base of an adult Black Oak usually have leaves near the base of the sucker which are simple in outline (Pl. 20, fig. 69), or slightly lobed and with small teeth (Pl. 20, fig. 70). Succeeding leaves become rapidly more lobate and bristly (Fig. 69), but do not acquire the full character leaves of the species (Pl. 20, fig. 71) for a considerable distance from the base. As Emerson ('46) says of the form of the leaves in this species, "* * * on young and vigorous shoots, particularly on sprouts from a stump, more nearly entire." Suckers from the base of the Scarlet Oak have leaves of the same form as in the Black Oak.

In the above oaks, then, in suckers and in vigorous growths from the stump, the leaves are more entire or simple than the typical leaves of the several species, thus making an approach to the simplicity of the seedling in a greater or less degree. The fossil oaks of the Cretaceous (Lesquereux, '91), and Tertiary are simple in outline or slightly toothed. The seedlings, suckers, etc., of the species discussed are therefore in their simplicity comparable to ancient fossil allies. As the Swamp White Oak and Chestnut Oak are simpler in outline than the Black and Red Oak types, they make a nearer approach to the characters of seedlings, suckers, and early fossil oaks, and may, therefore, be considered as the more primitive of our New England species. In the Live Oak of California (*Quercus chrysolepis* Lieb.), the Laurel Oak (*Q. imbricaria* Mich.), and the Oblong-leaf Oak (*Quercus oblongifolia* Torr.), according to Professor Sargent ('91–'97), the typical leaves are entire, being oval, oblong, or lanceolate in the several species. In vigorous shoots (also in the young of *Q. chrysolepis*), he says the leaves are often dentate or lobed. These and similar species at first sight appear to be primitive oaks, on account of the simplicity of their leaves, which in general are comparable to the simple leaves of fossil species and the young of specialized species. As vigorous shoots so frequently show reversionary characters, it suggests the view that these species may be simple from reversion not from primitiveness. A study of oaks from this point of view would be interesting.

MYRICA CERIFERA. Seedlings of the Bayberry (*Myrica cerifera* L.), were obtained from the Arnold arboretum. The cotyledons (Pl. 19, figs. 52, 52a) are broad, spathulate, distally emarginate, non-petiolate, 5.5 mm. long, 3 mm. wide. The first nepionic leaves are 6 mm. long, 4 mm. wide, broadly spathulate, with three distal dentations. The first four leaves are of the same form only increasing in size. In later leaves additional marginal indentations develop so that the leaf has a slightly lobate border; also a petiole develops, the blade extending down the petiole marginally.

In the adult the leaves are very variable, being entire or slightly toothed (Pl. 19, fig. 53). The midrib always extends at the tip as a slight mucronate point, in this feature resembling the tip of the early nepionic leaves. Very frequently two terminal indentations occur, when the leaf may be closely compared with the first nepionic leaves; frequently more indentations occur when in this feature it may be compared with later leaves of the seedling. As a whole it may be said that the later leaves of the seedling are more deeply dentate and in this character more specialized than the leaves of the average adult.

PINUS RIGIDA. The Pitch Pine (*Pinus rigida* Mill.) presents interesting localized stages. In the seedling the cotyledons are strong and vigorous (Pl. 21, figs. 72, 73). They vary in number from four to seven. In 100 seedlings counted, 18 had 4 cotyledons, 55 had 5 cotyledons, 26 had 6, and 1 had 7. Lubbock ('92) says that the Pitch Pine has from 4 to 6 cotyledons. The seven cotyledons found in one specimen are evidently somewhat rare, and may be anomalous for the species. The cotyledons are smooth and free from spinose growths, they are roughly triangular in section (Pl. 21, fig. 73b), and acuminate distally. The form of these cotyledons is attributed to their mutual contact and pressure during growth; compare Pl. 21, fig. 73b, with the White Pine cluster (Pl. 21, fig. 81a, b), where five leaves are brought close together during growth, inducing a similar triangular form. Succeeding the cotyledons, the young Pitch Pine is densely clothed with the nepionic or primary leaves. These leaves (Pl. 21, fig. 73) are linear, acuminate distally, flattened on the inner aspect and curved on the outer (Fig. 73a). On the borders or edges are two rows of delicate saw-like spines, pointing distally. No third row exists as in adult leaves. From about 13 to 20 mm. above the cotyledons the bundles of leaves typical of the species begin to appear in the axils of the primary leaves (Pl. 21, fig. 74). These bundles of leaves are usually in threes, but clusters are found in which two leaves occur instead of three; they are not very common, however. The first two or three primary leaves which bear axillary clusters of needles (Pl. 21, fig. 74a) are long and acicular, as are preceding primary leaves. Succeeding primary leaves, however, rapidly shorten, while retaining the leafy character; but within a short distance are reduced and represented only by rather prominent scales (Pl. 21, fig. 75), which subtend the leaf-clusters. During succeeding growth to the adult, scales normally occupy the same position at the base of leaf-clusters.

In the adult Pitch Pine the leaf-clusters are composed of three leaves, basally surrounded by a sheath (Pl. 21, fig. 75). From their packed condition during growth each leaf has assumed a form roughly triangular in section, but curved on the outer side. On the three edges (two lateral and one median) a series of fine saw-like serrations have developed similar to those seen in primary and secondary leaves of other pines. Mr. Charles E. Faxon informs me that he has seen a branch of this species in which all the leaves were in bundles of fives. As five leaves may be considered more specialized than three leaves, the typical condition in this species, such a branch may properly be considered a progressive localized variation.

When a young Pitch Pine has lost its leader or other prominent shoot, or, according to Emerson ('46) and Sargent ('91–'97), on stumps or after fire, a secondary sucker-like growth may be induced. These secondary growths are commonly vigorous (Pl. 21, fig. 76 and fig. 77), and the scales have taken on a leafy expansion. The leaves are long, acuminate distally, flattened on the inner and curved on the outer side; also they bear a row of saw-like teeth on the edges. They are thus seen to be closely similar to the nepionic primary leaves. These reversionary or localized primary leaves usually bear a bundle of leaves in their axils (Pl. 21, fig. 76), but the bundles in some cases may not develop, as shown in a few leaves in the figure. Rapid growths from the stump may be entirely composed of primary leaves (Pl. 21, fig. 77), the bundles not developing until later. Emerson ('46) says of the Pitch Pine, "Its stump throws up sprouts the spring after the stem has been felled. * * * The fallen trunk itself throws out sprouts in the succeeding summer; and the bundles of leaves of both are remarkable for issuing from the axil of a single leaf, in the same manner as is observed in the young plant." I have occasionally seen in a very limited way similar growths on adult trees, where no apparent cause existed. When young seedling plants throw out lateral branches close to the ground, it is found that such branches for a certain distance are clothed with primary leaves, as is the vertical axis at the area where they originated. This is in accord with what has been observed in many other cases; namely, that branches from nepionic areas are characterized by nepionic leaves, as in *Ampelopsis tricuspidata*, Negundo, ashes, oaks, Areca, etc.

In the Pitch Pine, then, we find nepionic characters repeated in localized parts, either as branches from the nepionic area, or abnormal growths from any portion of the plants, but especially from stumps and young trees which have lost their leader or other prominent branch.

While in normal growth the Pitch Pine loses its primary leaves very early, Sargent ('91–'97) says they may be retained for several years in the nut pines. In *Pinus quadrifolia* he says that after five or six years the primary leaves are shorter and begin to bear leaf-clusters in their axils. At Shady Hill nurseries plants of *Pinus densiflora* and *P. massoniana*, a foot or more in height, were seen which bore primary leaves with axillary leaf-clusters on all parts of the plants.

PINUS STROBUS. In the White Pine (*Pinus strobus* L.), seedlings (Pl. 21, figs. 78–80) have from seven to ten cotyledons, in specimens examined at the Arnold arboretum and Shady Hill nurseries. Out of eleven seedlings, four have seven cotyledons, two have eight, two have nine, and three have ten cotyledons. The cotyledons are large and strong, as in the Pitch Pine, which they resemble. There is one marked difference, however. In the White Pine the cotyledons are roughly triangular in section, and bear on their inner angle or ridge, also occasionally on their outer angles (Fig. 79a), fine saw-like teeth similar to the teeth of nepionic and adult leaves of this and other species. Similar teeth exist on the cotyledons of *Pinus monticola* Dougl. and Lamb, as observed at the Arnold arboretum. Serrations of the cotyledons of *Pinus strobus* are mentioned by Dr. Masters ('91), but have not been dwelt upon before. Such teeth do not exist in the cotyledons of *Pinus rigida*, *P. cembra* L., *P. resinosa* Aiton, or *P. pungens* Lamb. These teeth of cotyledons may be considered as a case of accelerated development in which features usually appearing first at a later stage are shoved back to an earlier, in this case an embryonic stage. Compare with *Eucharidium grandiflorum*, Figs. 1 to 3, page 103, which during growth acquires nepionic characters in embryonic leaves. The succeeding primary leaves of the White Pine seedling are similar to those of the Pitch Pine, but are retained longer than in that species; primary leaves are retained in the specimens observed until the plant is from 3.5 to 5 cm. in height, the end of the first year's growth. Then (Pl. 21, fig. 81) the primary leaves begin to shorten, and bundles of five leaves, characteristic of the species, are borne in the axils of the shortened primary leaves which are soon replaced by small scales. Primary leaves apparently never occur in later normal or abnormal growths of this species.

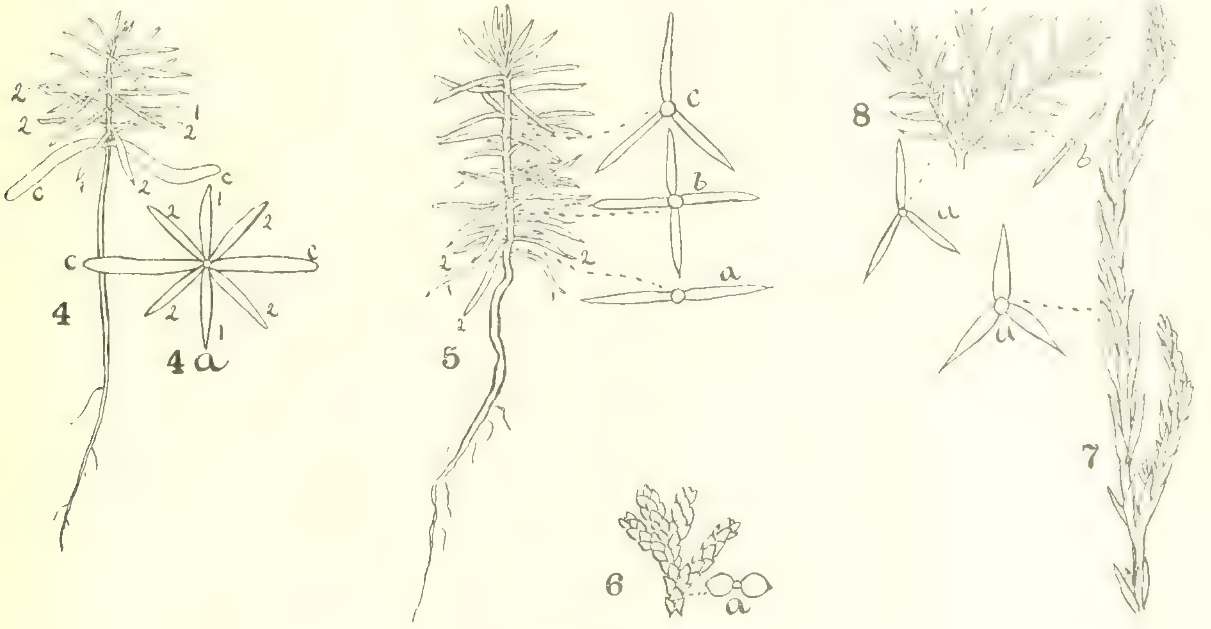
The leaf-clusters of the White Pine are enclosed in a very short sheath at the base (Pl. 21, fig. 81a); from mutual pressure they have taken on a triangular form (Figs. 81a, b), and the angles have saw-like teeth (Fig. 81a, c), as in the Pitch Pine.

In seedling pines the duration of the nepionic character of primary leaves varies greatly according to the species. Such nepionic characters may appear later in special localized growths under certain conditions, as described, but this again varies with species, not being a character common to all pines.

PINUS RESINOSA. In seedlings of *Pinus resinosa* Aiton, the features differ from those of other pines observed. The specimens were grown at the Arnold arboretum, one of them has 7 cotyledons, a second has 6; they are quite large, measuring 2 cm. in length. The primary leaves are unusually long, measuring 27–30 mm., and have fine serrate teeth on the lateral borders as in other species. The cluster-leaves are in twos, flat on their apposed borders, curved on their outer sides, with rows of fine serrate spines as in primary leaves. The first cluster of leaves in the seedling is in the axil of a primary leaf within 2 mm. of the cotyledons. Other axillary bundles occur throughout the length of the axis, which in the larger specimen measures 25 mm. above the cotyledons. The larger part of the primary leaves, however, do not bear axillary clusters. This species is peculiar in the size and luxuriance of the primary leaves, in the early introduction of bundles of leaves, and in the relatively small number of such bundles to the number of primaries during early growth.

LARIX. Of the Larch I have only seen one young seedling which was kindly sent me by Mr. Charles E. Faxon. This seedling, *Larix occidentalis* Nutt. (Pl. 21, fig. 82), has five cotyledons, quite similar to those of the pine. Succeeding the cotyledons the nepionic leaves are thickly distributed on the ascending axis, but not so thickly as in the pines. These nepionic leaves are narrow, linear, acuminate distally. In the adult Larch, as represented by *Larix europaea* DC. (Pl. 21, fig. 83), the leaves are given off in dense clusters on the old wood. In the new wood of the current season's growth, on the other hand, there are no clusters, but the leaves are given off singly along the axis, as in the seedling. The current season's growth of this tree, then, resembles closely the nepionic growth of the seedling. A similar condition has been observed in other cases, where the new growth of the current year resembles the young. This is especially marked in *Ampelopsis tricuspidata* as described.

JUNIPERUS VIRGINIANA. In the Red Cedar (*Juniperus virginiana* L.) the later stages in development and the features of the adult are very striking. Young seedlings were found in comparative abundance near adults in July and August, both at Martha's Vineyard and Milton, Mass. The seedling, Fig. 4, has two relatively broad, strap-shaped cotyledons, which are thin and very fugitive. While the number of cotyledons is variable in many conifers, I have seen no variation in this species, and two seem to be a constant character in the cypress family. The next or nepionic leaves differ from the cotyledons in that they are shorter, narrower, thicker, distally acuminate, and more permanent. The first nepionic leaves are a whorl of two opposite leaves, alternating with the cotyledons (Figs. 4, 4a). They are of the shape described, and about 7 mm. long. This two-leaved stage, in all the numerous individuals observed, is limited to a single pair of leaves. The next stage is introduced by a whorl of four leaves which are so arranged that they alternate with the cotyledons and first whorl of two nepionic leaves (Figs. 4, 4a). Thus up to and including the second nepionic whorl no leaves of the seedling are vertically superimposed. The second whorl of four leaves alternates with the first whorl and therefore lies above the cotyledons and pair of first nepionic leaves. Other whorls of four leaves succeed the first two, occupying a vertical space of from 6 to 26 mm., and including



JUNIPERUS VIRGINIANA.

4. Seedling, showing two long, broad cotyledons, c; nepionic leaves; 1, whorl of two leaves alternating with cotyledons; 2, whorl of four leaves alternating with cotyledons and first whorl of two leaves, followed by whorls of four leaves throughout this stage. × 1.5. 4a, plan of arrangement of cotyledons and first two nepionic whorls. Milton, Mass.

5. Older seedling, showing two-leaved and four-leaved whorls, followed by a stage with three-leaved whorls as represented in diagrams a, b, c. × 1.5.

6. Typical leaves of adult in alternating two-leaved whorls. × 1.5. a, plan of leaf arrangement.

7. Elongate vigorous growth of a terminal branch of adult, showing long, broad leaves arranged in three-leaved whorls. × 1.5. a, plan of same.

8. Abnormal tufted ("bird's-nest") growth of adult, showing elongate leaves arranged in three-leaved or two-leaved whorls. × 1.5. Compare with Fig. 5. a, b, plans of same.

Figs. 5–8, West Chop, Martha's Vineyard, Mass.

five or six or more whorls. The four-leaved whorls mark the second nepionic stage. While this four-leaved whorl is characteristic of the vertical axis, such whorls have not been seen on any of the branches, even if given off very early. In *Thuya occidentalis*, *T. gigantea*, and *Libocedrus decurrens* (Pl. 22, figs. 86, 87, 89) the two cotyledons are also succeeded by one whorl of two leaves, then whorls of four leaves as described later. A third nepionic stage in the Red Cedar is marked by another change. The four-leaved whorl is abandoned, and the leaves are arranged in whorls of threes (Fig. 5). This occurs as early as 6 mm. above the two-leaved stage in some cases, or a little later in other cases. When the three-leaved stage is introduced, no more four-leaved whorls are formed. Occasionally branches on young plants have two-leaved whorls; these may be limited to two or three whorls only, or may be of greater extent. While such occur, they are less common, and three-leaved whorls are the characteristic feature of this period of development. The leaves are flat, narrow, acuminate, distally ending in a sharp point, and they are about 8–10 mm. long. This three-leaved acicular character has been observed by several naturalists; it is retained until the tree attains the height of a foot or more, when adult characters appear, but the period of their introduction varies greatly in individuals. In the adult the typical leaves are arranged in pairs, alternating in successive whorls (Fig. 6). The leaves are blunt, scale-like, and closely imbricating.

The above gives the features of leaves in the normal progressive development of the Red Cedar. In the adult, variations are striking, as described by Emerson ('46), Sargent ('91–'97), and others. In vigorous shoots (Fig. 7), given out mainly at the ends of branches, the leaves are broad, elongate, distally acuminate, and arranged in whorls of three or two leaves; but the former or ternate arrangement is perhaps the more common. The dense tuft-like growths of adult Red Cedars, called "bird's-nests," are still more obvious. They are caused by the growth of a fungus, *Gymnosporangium nidus-avis* Thaxter ('90), and are common at points where an injury has taken place, as the cutting of a branch, on feeble or stunted trees, also on otherwise healthy trees. It is distinctly a pathologic character. On these growths the leaves are long and needle-shaped (Fig. 8), and closely resemble the leaves of the young (Fig. 5). The leaves on these tuft-like growths may be arranged in whorls of twos or threes; but three-leaved whorls are present to a greater or less extent on all such growths and often predominate. At West Chop, Martha's Vineyard, Mass., the soil is excessively barren and the situation exposed. There the "bird's-nest" growths on the stunted cedars are very abundant. The leaves on these, as in the vigorous terminal growths, are largely arranged in whorls of three leaves. In Milton, Mass., where the soil is fertile, "bird's-nest" growths are less common, and both in these and in vigorous growths two-leaved whorls predominate over three-leaved whorls. At Cohasset, Mass., where the soil is good but the situation exposed, the ternate arrangement prevails in "bird's-nest" growths. On sickly branches or decrepit, dying trees similar needle-shaped leaves are often produced. I have seen old trees, almost bare stumps, but with the few remaining leaves of the typical awl-form characteristic of the young. There is, then, in the Red Cedar a clear case of pathologic localized stages which repeat youthful or primitive characters. It is a suggestive fact, as has been pointed out by Emerson ('46) and others, that the acerose ternate leaves seen in the young and localized pathologic parts of the adult Red Cedar are closely like the condition seen in the prostrate Juniper (*Juniperus communis* L.). This allied species, on account of its awl-shaped, bristly, ternate leaves and prostrate habit, we may suppose to be either a primitive or a degradational species, perhaps more likely the latter. The fastigiate form of *J. communis*, or Irish Juniper, has similar ternate bristly leaves. Another species, *Juniperus californica* Carr., has ternate leaves, but appressed, not elongate and awl-like (Sargent, '91–'97).

The earliest known fossil cedars from the Cretaceous have acerose, ternate leaves. These ancient, primitive types apparently represent the ancestral form from which the acerose, ternate leaves of the young Red Cedar are derived, and to which the similar leaves of pathologic growths of adults are reversions. *Juniperus communis* has retained the primitive acerose, ternate type, or else has reverted to it. *Juniperus californica* has retained the primitive character of ternate arrangement of the leaves, but has appressed leaves, and in this feature is in accord with the progressive species of the genus.

JUNIPERUS MONOSPERMUM. Of *Juniperus monospermum* Engel. I had the opportunity of seeing six seedlings at the Arnold arboretum. The seed were collected in Manitou, Col. All of the seedlings had two cotyledons, succeeded by a whorl of two leaves, again succeeded by whorls of four leaves as in *J. virginiana*. In five of the specimens, four-leaved whorls continued to the top of the main stem (a few inches only), but the leaves of the lateral branches were all in whorls of threes. In one of the specimens there were three-leaved whorls on the upper part of the main stem, showing a transition similar to that shown in *Juniperus virginiana* (Fig. 5).

THUYA OCCIDENTALIS. An interesting series of seedling Arbor Vitae (*Thuya occidentalis* L.), was sent me from Beedes, Adirondacks, N. Y., by the kindness of Miss Marian C. Jackson. Only one of these was young enough to show cotyledons and the first succeeding leaves. In this specimen (Pl. 22, fig. 84) there are two strap-shaped cotyledons. The first nepionic leaves are a whorl of four leaves, 4 mm. long, alternating in position with the cotyledons, as shown diagrammatically in Pl. 22, fig. 84a. The second whorl is also composed of four leaves alternating with the first whorl. Succeeding leaves in this and most specimens are in whorls of two leaves, no four-leaved whorls occurring in later growth, and no three-leaved whorls appearing at any stage.

Two specimens of seedling Arbor Vitae, growing under a hedge in cultivation at Andover, Mass., were collected by Mrs. R. T. Jackson. In both specimens, the first leaves succeeding the cotyledons are a pair of opposite leaves. In one of the specimens (Pl. 22, fig. 86), the second whorl is four-leaved, and succeeding leaves are in whorls of threes on the main stem; but a lateral branch has leaves in twos only. The second specimen has three leaves in the second whorl; but it is evidently a four-leaved whorl in which one leaf is suppressed, or lost in early growth, as a space exists where it should occur. Later leaves of this specimen are arranged on the main stem in irregularly placed threes, they not being sufficiently in the same planes of insertion to call them whorls. On a side branch the leaves are in twos as usual. In a seedling figured in Professor Sargent's Silva, there are two cotyledons succeeded by a whorl of two leaves, then by several whorls of four leaves. While considerable variation occurs, it is evident that the typical seedling has two cotyledons succeeded by a whorl of two leaves, then by one or more whorls of four leaves succeeded by the two-leaved whorls characteristic of this type. The variations are no greater than those described later in *Libocedrus decurrens.*

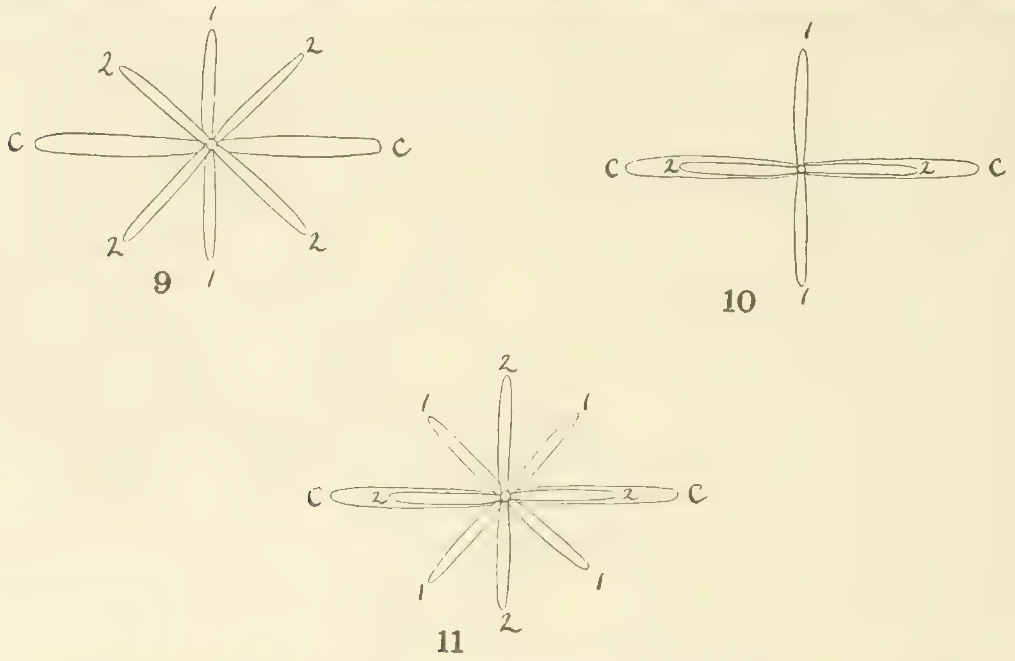
To return to the specimen of Arbor Vitae (Pl. 22, fig. 84), the narrow, elongate, primary leaves are maintained to the tip of the main stem, and the same feature exists in all the other seedlings; concurrently lateral branches have already acquired leaves which are a close approach to the adult condition. This is a noteworthy feature, for in many conifers, *Pinus rigida*, Fig. 74, Libocedrus, Fig. 89, the main stem develops mature features first, or at least as soon as lateral branches. On the side branches (Pl. 22, fig. 84), at their inception, there are one or more pairs of typical primary leaves; but these soon give place to leaves which are shorter, appressed, scale-like. Succeeding pairs of leaves (Pl. 22, fig. 84b) differ, as do adults, in that the marginal leaves are narrow, embracing by their apposed edges the median pairs which are flattened, broadened and embraced by the distal borders of the preceding marginal pair. These leaves of young branches are acuminate distally, with free tips, whereas in the adult (Pl. 22, fig. 85) the tips of the leaves are blunt and appressed. It is an interesting phylogenetic fact, that in fossil Thuyites from the Jurassic, the tips of the leaves are acuminate and distally free as in the young of our species (Fig. 84b).

The features as described are characteristic of 35 out of 40 seedlings of this species from the Adirondacks; 5 specimens only showed a variation. In three of these the leaves are in whorls of threes up to within two or three whorls of the introduction of "character" leaves, when two-leaved whorls appear. Two other specimens have respectively 14 and 17 whorls of three leaves each, above which the leaves are in twos as usual. It is to be remembered, as stated, that only one specimen showed cotyledons and first succeeding whorls. This taking on of a three-leaved whorl in a type which is so strongly two-leaved is striking. On leading shoots of adult Arbor Vitae pointed leaves sometimes occur, often a quarter of an inch in length (Sargent, '94: 57), showing localized reversions to the youthful and ancestral condition. These elongate leaves are not so common or so marked in character as are the somewhat similar reversionary leaves of the Red Cedar.

THUYA GIGANTEA. The seedling of the western species of Arbor Vitae (*Thuya gigantea* Nuttall) differs markedly from the seedling of *T. occidentalis*. In this species (Pl. 22, fig. 87), as shown by two specimens, there are two cotyledons 7 mm. long, 2 mm. broad. The first nepionic leaves are a single pair, very short, 2 mm. long, lying close above the cotyledons, and alternating with them in position. In the second whorl there are four leaves, considerably larger and alternating with the first pair and cotyledons, as shown in the diagram (Pl. 22, fig. 87a). Succeeding leaves on the main stem are in four-leaved whorls until very near the top where they become somewhat irregular. This is a marked difference from *Thuya occidentalis* (Figs. 84, 86) in which no four-leaved whorls occur after the second nepionic whorl. Primary leaves are borne on the main stem for a considerable period after "character" leaves have made their appearance on the branches, as in *Thuya occidentalis*. The branches are more delicate and more erect, forming a smaller angle with the main stem than in *Thuya occidentalis*, where branches form almost a right angle with the main stem and are somewhat pendulous. On the branches of *Thuya gigantea* there are two or three whorls of primary leaves; but they are in twos instead of fours as on the main stem. The character leaves are narrower and more pointed than those of *T. occidentalis*, but as in that species they are comparable to the leaves of the Jurassic species of Thuyites. In the adult the leaves have lost the acuminate tips seen in seedlings (Fig. 87) and are appressed. The specimens described are seedlings from the Arnold arboretum raised from seeds collected at Ashford, Washington.

LIBOCEDRUS DECURRENS. Seedlings of *Libocedrus decurrens* Torrey present interesting features of development and variation. There were 25 seedlings in the lot studied, raised at the Arnold arboretum from seed collected in Oregon; all were grown under the same conditions. The seed were planted, Mar. 28, 1898, and seedlings were studied, Sept. 17, 1898. The typical condition is represented in Pl. 22, figs. 88, 89. There are two long, strap-shaped cotyledons, 30 mm. long and 3 mm. broad. The first nepionic leaves are a pair 12 mm. long and .75 mm. broad, lying close to and alternating with the cotyledons. Succeeding the two-leaved whorl after a considerable interspace there is a four-leaved whorl which alternates with the first whorl and cotyledons (Fig. 9). Succeeding leaves are all in four-leaved whorls and are narrow, acicular, but large and vigorous and of a bluish green color. Fig. 88 represents a plant in which all the leaves are primaries, but in Fig. 89 it is seen that character leaves develop early, and at about the same period of growth, both on the terminal shoot and side branches. Side branches bear a few whorls of primary leaves in fours: but very soon the later form of leaf is introduced. The leaves of this late nepionic stage are appressed, sharp-pointed (Pl. 22, fig. 89a), arranged in four-leaved whorls, the marginal leaves narrow, elongate, and embracing the median pair. The arrangement is similar to that of Thuya, Fig. 84b, but with the essential difference that in Thuya the leaves are two-ranked and marginal leaves embrace the edges of the leaves of the next succeeding whorl. In adult *Libocedrus decurrens* (Fig. 90) the leaves are appressed, blunt distally, and in four-leaved whorls as in the later stages in the young.

The variations in the seedlings are quite striking. Out of twenty-five specimens, 22 conformed to the type as described. Two specimens had skipped the two-leaved stage, the first whorl of leaves after the cotyledons being a four-leaved whorl (Fig. 11, and Pl. 22, Figs. 91, 91a). It is noteworthy in both of these specimens that the two leaves of either side are fused proximally and for a slight distance (2 mm.) upward from their point of insertion on the stem (Figs. 91, 91a). This suggests the view that the four-



LIBOCEDRUS DECURRENS.

9-11. Plans of comparative phyllotactic arrangement of cotyledons, c, and first two whorls of nepionic leaves, 1, 2.

9. Typical arrangement, in which there are two leaves in the first nepionic whorl and four leaves in the second nepionic whorl, seen in Pl. 22, figs. 88, 89.]

10. Abnormal arrangement in which there are only two leaves in the second nepionic whorl, seen in Pl. 22, fig. 92.

11. Abnormal arrangement in which there are four leaves in the first as well as in the second nepionic whorl, seen in Pl. 22, fig. 91, 91a.

leaved condition of this individual whorl is morphologically a splitting of the normal two leaves characteristic of this stage. In relative phyllotactic arrangement this first whorl in relation to the cotyledons occupies a similar position to the second whorl of the normal growth; compare Figs. 9 and 11. The second whorl occupies the same position as the third whorl in normal growth.

The second specimen mentioned as having a four-leaved whorl succeeding the cotyledons has an arrangement as in Fig. 91, excepting that the third whorl above the cotyledons consists of an isolated two-leaved whorl and is the only such variation observed.

A third specimen showing variation from the normal is represented in Pl. 22, fig. 92. In this all the primary leaves are two- instead of four-ranked; but the later character leaves are four-ranked as usual. The first pair of leaves alternates with the cotyledons as usual. The second pair alternates with the first and overlies the cotyledons, Fig. 10. Succeeding pairs of primary leaves are regularly alternated (Pl. 22, fig. 92). The phyllotactic arrangement of leaves in the normal and aberrant seedling is seen by comparing Figs. 9–11. The varying arrangement of the leaves in these several seedlings shows how sensitive the growth force of these plants is to the relations of environment, each set being arranged so that the first whorl alternates with the cotyledons and the second whorl alternates with the first, covering the cotyledons or not as the case may be.

Youthful characters are considered of phylogenetic significance, barring larval adaptation and skipping of stages by acceleration of development. It is seen that in the young of Juniperus, Thuya, and Libocedrus, succeeding the cotyledons there is typically a whorl of two leaves, succeeded by one or more whorls of four leaves. In *Cupressus lawsoniana* Murray, according to the figure in Professor Sargent's Silva, the nepionic leaves are all in whorls of fours. These should point to primitive radicals which in the adult condition are characterized by a similar arrangement. Of the two-leaved stage no ancestral form can be pointed out at present. It would seem that Thuya, Cupressus, and Juniperus may be considered degradational types which in the adult in typical species have reverted to the two-leaved type characteristic of some ancestral form, as evinced by stages of their own young. The degradational character of these genera is evinced by the depauperate scale-like leaves as well as the two-ranked arrangement. The adult representative of the young four-leaved stage of these genera, it seems, may be represented by the type Libocedrus or more properly a predecessor of the same, which had four-ranked needle-like leaves. Libocedrus is not known earlier than the Cretaceous, and these old forms are quite close to the modern representative, but its four-ranked arrangement is so striking that it would seem to indicate that it is in the line of ancestry of the associated genera.

PALMS. Amongst palms many species present interesting features of localized stages in development. I have studied the development of seedling palms of thirty-seven species, and from published figures of von Martius and others know something of the early characters of about forty-five species, distributed through twenty-eight genera. Seedlings of all species have simple, early seed-leaves, and these are always one of two types. The first and most primitive type of seed-leaf is elongate, lanceolate, or oval, terminating more or less acutely, and with a longer or shorter rachis, usually long. This type is seen in Latania (Pl. 23, fig. 94), Corypha (Pl. 23, fig. 104), Cocos (Pl. 23, fig. 102), Phoenix (Pl. 23, figs. 100, 103, 103a) and many other genera. The second type of nepionic or seed-leaf is similar to the first, except that it is distally cleft. It is characteristic of Chrysalidocarpus (Pl. 23, fig. 95), Kentia (Pl. 23, fig. 96), Caryota (Pl. 23, fig. 98), and of many other genera. Very young specimens of genera which have distally cleft leaves or exceptional individuals show a transient distal fusion of the apices of the leaf, as in Kentia (Pl. 22, fig. 96), demonstrating that the cleft type is only a modification of the first or entire type. In some types, as *Stevensonia grandifolia* J. Dunc. (*Phoenicophorum sechellarum* H. Wendl.), which have distally cleft leaves, the first leaves are entire, the cleft character appearing later (third leaf of the specimen in hand). This is a further demonstration of the primitive nature of the entire type. In some cases the acuminate tips of seed-leaves may be modified by distal truncation, as in *Arenga saccharifera* Labill. and *Caryota cumingii* Lodd. (*C. urens* Blanco.) (Pl. 23, fig. 98).

A fossil species from the Cretaceous (Laramie), *Oreodoxites plicatus* Lesq., closely resembles the form of the more primitive type of seed-leaf, and hardly differs, except in its greater size, from the young leaf of Corypha (Pl. 23, fig. 104). Other fossil palms from the Cretaceous and Tertiary belong to genera the young of which is characterized by the entire type of leaf.

In *Latania commersonii* J. F. Gmel. (*L. borbonica* Lam.), the seed-leaf is ovate, lanceolate (Pl. 23, fig. 94): during growth the later leaves become relatively broader, until, by distal tension, splits take place (Pl. 23, fig. 93), and in the adult the leaf is a quite broad, fan-leaf type. The development of other fan-leaf palms, as Sabal, Washingtonia, Chamaerops, and Raphis, is similar to that of Latania. The angle of divergence of the rays varies directly with the relative length of the rachis and the amount of leaf-tissue formed.

In *Phoenix canariensis* Hort. the first seed-leaf (Pl. 23, fig. 100) is elongate, lanceolate. The first leaves of *Phoenix rupicola* T. Anders. are similar; in later added growth the leaves, while retaining their simple outline, become relatively broader, with an elongate rachis, as shown in leaf 1, Pl. 23, figs. 103, 103a. During growth, as new leaves are added, the rachis elongates, the leaf-tissue on the sides becomes relatively reduced, and pinnae result from the splitting apart of the leaflets, as shown in leaves 2 and 3 of Fig. 103. The leaf of the adult is similar to the last formed leaf in Pl. 23, fig. 103, except in the increase in size, and in the number of pinnae, and in the relative reduction of the terminal leaflet. In *Cocos weddeliana* Wendl. (Pl. 23, figs. 101, 102), the development is similar to that of Phoenix.

In *Caryota cumingii* Lodd. (*C. urens* Blanco) (Pl. 23, figs. 97–98), the early seed-leaves are deeply cleft, more so than in the seedling of any other palm known, and the leaf is distally truncate and serrate as if snipped with scissors. As the plant grows older, the leaves become pinnate (Pl. 23, fig. 97), the distal leaflet resembling the simple early leaf. Adult leaves are similar to this early compound leaf, except in size and the increased number of the leaflets. This is, perhaps, the most differentiated type of nepionic leaf seen in palms, and in its characters shows a markedly accelerated development. *Caryota rumphiana* Mort. is similar to *C. cumingii* in early characters.

In palms with pinnately compound leaves, in all cases where the adult and young are known to me, the distal leaflet of the adult leaf corresponds closely in form to the whole of the early nepionic leaf. This is the case in several species each of Phoenix (Pl. 23, figs. 100, 103), Cocos (Figs. 101, 102), Caryota (Fig. 97, 98), Chrysalidocarpus (Fig. 95), Kentia (Fig. 96) and other genera.

In the growth of a pinnate-leaved palm, when a new leaf first appears, the pinnae cling together laterally on their outer margin and to the distal leaflet, in such a way that the whole leaf simulates the entire type and demonstrates the simple dynamic genesis of this type of compound leaf from an ovate leaf like that of the young. This is shown well in *Diplothemium maritimum* Mort. (Pl. 23, fig. 99), also in part of the leaflets of Phoenix (Fig. 103, leaf 3) and Cocos (Fig. 101). A similar clinging may be seen in palmate palms (Pl. 23, fig. 93). An elongation of the rachis with attendant reduction of leaf-tissue induces the pinnate type. A shortening of the rachis induces the palmate type; Sabal, Latania. An extreme shortening of the rachis with abundant leaf development may even induce a form in which the leaf is radial from a central point in the rachis; some species of Chamaerops. In the development of a leaf, then, there is in this localized part a repetition of features seen in the young. Also the distal tip of pinnate leaves repeats the form of nepionic leaves.

Some palms sucker from the base, and in such suckers we might expect to find localized stages in development, as is the case. In *Raphis flabelliformis* L'Herit., a fan-leaf palm, suckers from the base have simple ovate leaves like (Pl. 23, fig. 94) and only in later growth are the typical fan-leaves of the species acquired. I have not seen seedlings of *R. flabelliformis*, but the suckers repeat the form of seedlings of *Raphis humilis* var. *elegans* and allied genera so closely that in leaf characters they are inseparable.

In *Chrysalidocarpus lutescens* (Bury) Wendl. (*Areca lutescens* Bury) (Pl. 23, fig. 95), and *Kentia balmoreana* (Pl. 23, fig. 96), the seedling has first a simple distally cleft leaf, succeeded in later growth by pinnately compound leaves, the distal end of which resembles the first simple leaf. In the adult the compound leaf has numerous leaflets, but otherwise differs from the compound leaf as figured here only in the relative reduction of the terminal leaflet. Suckers of *Chrysalidocarpus lutescens* repeat the form of the seedling so closely that they are practically identical in leaf characters.

FERNS. Ferns on account of their usually compound leaves should show evidences of localized stages in development. While in higher plants the tip of the leaf is formed first, and is early transformed into permanent tissue (p. 93), a different condition occurs in ferns. In ferns the apical growth continues and in many genera is even unlimited, the apex being always capable of further growth (Sachs, '75). In spite of this radical difference in method of growth, the tips of ferns are usually simpler than the proximal portions and in so far they resemble the condition seen in the young.

The individual leaflets of Adiantum are similar to the whole frond of the young, which in an early stage is composed of a single leaflet. The tip of the frond of *Onoclea sensibilis* L. is entire and in so far resembles the whole frond of the young, which is also entire, though relatively broader and orbicular.

A young plant of the common Brake (*Pteris aquilina* L.) has a very simple type of frond as compared with the adult. Such a young specimen, of which the frond is 6.5 cm. high, is shown in Pl. 23, fig. 105. The distal tip of this frond is entire; passing proximally, the frond becomes pinnatifid and then once pinnate. The pinnae are themselves distally entire, as is the tip of the frond; but passing proximally they become pinnatifid. This plant, although young, shows the remains of several fronds preceding the one figured. Somewhat older specimens have similar characters, but more advanced. The frond of adult *Pteris aquilina* is twice or thrice pinnate with three primary divisions. The simplest parts of the frond are at the distal ends of the primary divisions, the most complex parts are at the proximal ends of the same. The several divisions of the frond are entire at the distal end, becoming more or less divided proximally. The distal end of the primary divisions closely resembles the whole frond of the young plant (Pl. 23, fig. 105).

LOCALIZED STAGES IN DEVELOPMENT IN ANIMALS.

Turning to the animal kingdom, there are some groups which present interesting phases of localized stages in development. In the asexual reproduction of animals by budding, a new individual is produced in a manner which, roughly speaking, may be compared to the reproduction of plants by suckers. Such youthful zooids one would expect to repeat more or less the characters of the young from the egg, and these are [illegible] cases of localized stages in development.

HYDRA. In Hydra, when the bud is first formed, it is a simple outgrowth of the body walls. As a new mouth breaks through and tentacles are formed, the growing Hydra passes through stages of development which may be compared with the later stages seen in a Hydra produced from the egg. In the budding of other Hydrozoa and Actinozoa, the buds, when first formed, are simple, and during growth acquire their full specific (or specialized in the case of specialized zooids) characters. Clark ('65) figures the buds of Hydra, and describes the buds of a sea-anemone. In the latter, he says the buds are at first simple outgrowths, as in Hydra; later a mouth and tentacles appear. At an early stage there are only six of these tentacles.

GALAXEA CAESPITOSA. In a large specimen of *Galaxea caespitosa* Dana, from Singapore, in the collection of the Boston society of natural history, there are many young corallites budded out from the coenenchyma. In the youngest of these buds (Pl. 24, fig. 106), there are only six septa. One of the septa is shorter than the others, probably due to a break. In an older bud (Pl. 24, fig. 107) additional septa have appeared between the six primaries. A still older specimen (Pl. 24, fig. 108) shows a further development of the six primary septa; the secondary septa have also grown. In an adult corallite from the same specimen (Pl. 24, fig. 109), the first twelve septa, including the primaries and secondaries, have met and fused in the center. Additional tertiary septa exist between the older septa, and are individually comparable to the early condition of the primary and secondary septa, as seen in Figs. 106–108.

The budding method of acquiring characters which repeat stages seen in later development from the egg, is distinctly a form of localized stages in development. It is quite different, however, from the cases given of localized stages of development in other animals, where the repetition of characters is seen in parts serially added during the growth of one individual.

CRINOIDEA. In crinoids, the stem grows by increase in size of the plates, more or less throughout its length, and also by the intercalation of new plates between the calyx and topmost plate of the stem, or in that immediate vicinity. It is, therefore, seen that plates near the calyx are the youngest plates throughout the life of the individual.

In the recent *Metacrinus rotundus* Carp. from Japan, the plates close under the calyx are strongly pentagonal; they are also thickly clothed with cirrhi (Pl. 25, fig. 124). In the older portion of the stem (Fig. 124a), the plates have increased in size, are nearly circular in section, and the cirrhi occur as quite widely separated whorls.

In the recent *Pentacrinus decorus* Wy. Thoms. a similar condition exists. The plates close under the calyx are pentagonal and farther down are nearly round. In this species the cirrhi close to the calyx are not so abundant as in *Metacrinus rotundus*. In the Jurassic *Pentacrinus* (*Extracrinus*) *briareus* Quenst. the stem is pentagonal throughout its length (Pl. 25, figs. 125, 125a), and is densely clothed with cirrhi. Other species of Jurassic Pentacrinus also have pentagonal stems, as *P. basaltiformis* Miller (Pl. 25, fig. 126). The young last formed pentagonal plates of modern Pentacrinus and Metacrinus throughout life, therefore, bear a close resemblance to the whole stem of their ancient fossil representatives.

In *Platycrinus symmetricus* Wachs. and Spring. (Pl. 25, fig. 127), from the Subcarboniferous, and other species of the genus, the plates of the stem are oval in cross-section, and set on one another in such a manner that the axes of each plate are slightly different from those of the preceding plate. The result is a spirally twisted stem. On examining the young plates close under the calyx, it is seen that they are circular and smaller than the older plates of the stem. During growth, as new plates are added, the round plates grow and take on the oval and spiral form of the older plates of the stem. Whatever the ancestry of Platycrinus, it is probable that it came more or less directly from forms with a simple circular type of stem plate similar to that which is seen in the young plates close up under the calyx.

In crinoids, as in starfishes, the arms grow by the addition of new plates at the distal ends. As a consequence, the plates at the proximal end of the arm were formed first in the ontogeny of the individual and the plates at the distal ends of the arms are the youngest or last added plates.

In *Encrinus liliiformis* Mill., of the European Triassic, the plates at the base of the arms are monoserial, or arranged in a single row, each plate extending across the arm. Passing outward, the arm plates take on a biserial arrangement, the plates extending only half way across the arm; this condition is characteristic of the greater part of the length of the arm. As observed by Mr. A. W. Grabau, the plates at the tips or youngest portion of the arms are monoserial, in this feature resembling the oldest or first formed plates at the base of the arms. During the development of these plates at the tips of the arms, as shown by a series of specimens, the plates become relatively shortened, cease to pass entirely across the arm, and take on a biserial arrangement, like the plates on the intermediate portion of the arm.

ECHINI. Certain sea-urchins show localized stages in development in a typical way. In the growth of the sea-urchin newly added plates of the corona are introduced at the dorsal border between the genital or ocular plates and the last formed plates of the ambulacral or interambulacral areas. Therefore the plates at the dorsal portion of the corona are the youngest or last added plates, and other plates of the corona are progressively older as we proceed ventrally to the peristome.

STRONGYLOCENTROTUS DROBACHIENSIS. As shown by Lovén ('92), the interambulacral plates of *Strongylocentrotus drobachiensis* (O. F. M.), are marked at a very early stage by a single large spine boss (Pl. 24, fig. 112). An older specimen, Fig. 113, shows an extensive resorption of the first interambulacral plate, caused by the encroachment of the peristome, and a second spine boss on the third plate of the right-hand column. The simplest condition is at the ventral border, and passing dorsally during growth new features are progressively added. This same method of adding structural features has been demonstrated in many Palaeozoic Echini by Dr. T. A. Jaggar, Jr., and the author ('96).

In a series of *Strongylocentrotus drobachiensis* from Massachusetts Bay a sequence of stages in the development of plates has been followed. In the youngest of these specimens measuring 7 mm. in diameter (Pl. 24, fig. 114), there are eleven plates in each column of interambulacral plates. The plates of the ventral portion are ornamented by a primary and several secondary spine bosses. The last formed or eleventh plate is simpler, has only a single spine boss, and thus resembles all the plates of the very young individual (Pl. 24, fig. 112) and the youngest or last added plates of the older individuals (Pl. 24, figs. 115, 116). An older specimen (Pl. 24, fig. 115) measuring 25 mm. in diameter has sixteen plates in the interambulacral columns. The topmost or youngest plate of the right-hand column is very young and is smooth, having no spine bosses. This feature is not shown in any of the other figures of this species, but is characteristic of the plates of very young sea-urchins. The youngest or sixteenth plate of the left-hand column has one primary spine boss resembling the eleventh plates of Fig. 114 and all the plates of Fig. 112. The eleventh plate from the base of Fig. 115, which may be compared with the eleventh plate of Fig. 114, differs from that plate in having many secondary spine bosses in addition to the primary boss. In the growth of the sea-urchin the peristome increases in size by the enlargement of the plates of the corona and also (in most sea-urchins) by more or less resorption of the ventral border of the corona. The ratio of enlargement by the growth of plates and ventral resorption of the same is not at present known, and it is possible that one or more plates of Fig. 114 would have been resorbed before the specimen attained the size of Fig. 115. The eleventh plate of Fig. 115 is not therefore certainly the exact equivalent of the eleventh plate of Fig. 114. It may be the equivalent; but if not, it is a younger, not an older, plate than any represented in Fig. 114, so that for present purposes the comparison of these plates is applicable.

In an adult specimen, Fig. 116, measuring 52 mm. in diameter, there are twenty-two plates in the left interambulacral column. We find again that the youngest or twenty-second and twenty-first plates have a single spine boss and resemble the sixteenth plate of Fig. 115, the eleventh plate of Fig. 114, and all the plates of Fig. 112. It is also seen that the sixteenth plate, which has one spine boss in Fig. 115, has several in Fig. 116. The eleventh plate of Fig. 114 has one spine boss, the eleventh plate in Fig. 115 has in addition several secondary bosses, and in Fig. 116 the eleventh plate has yet more spine bosses, showing a still further development or specialization in the growth of plates which are actually or at least very nearly the equivalent of one another.

In this specimen of Strongylocentrotus, Pl. 24, fig. 116, the primary, secondary, and tertiary spine bosses are represented, but still smaller bosses or miliaries are omitted as an unnecessary and confusing amount of detail. In Fig. 116a, however, all the spine bosses are represented which occur in the fifteenth plate of the left-hand column of Fig. 116.

In the growth of this sea-urchin it is interesting to note that the increase in size is attained by the increase in the size of plates rather than by the increase in the number of plates. The smallest specimen, Fig. 114, measures 7 mm. in diameter and has 11 plates in a column, whereas the adult measures 52 mm. and has only 22 plates in a column, or twice as many as it had when about one seventh of the size attained.

ARBACIA PUNCTULATA. In *Arbacia punctulata* Gray, a similar series of facts may be observed and is especially clear on account of the relative simplicity of the interambulacral plates. A small individual, 23 mm. in diameter (Pl. 24, fig. 110), has eleven plates in each column. The eleventh plate of the left column is very young and has not yet acquired a spine boss; this is a common character of very young plates at this dorsal area in sea-urchins and is similar to the condition seen at the introduction of plates in embryonic sea-urchins (Lovén, '92, p. 11, Fig. 1). The tenth plate of this specimen has a single spine boss. Passing ventrally it is seen that plates 9, 8, 7 also have a single spine boss, but progressively larger. The sixth plate and others ventrally as far as the second plate all have two spine bosses. In an adult specimen measuring 45 mm. in diameter (Pl. 24, fig. 111), there are fourteen plates in each column. The fourteenth plate of the left column is small and has no spine boss, as in the eleventh plate of Fig. 110. The thirteenth plate has developed one spine boss and in this character is comparable to the tenth plate of Fig. 110. Passing ventrally it is seen that the tenth plate has two spine bosses, whereas the tenth plate of Fig. 110 has only one spine boss. The eighth, seventh, and sixth plates have each three spine bosses, whereas the similar plates in Fig. 110 have either one boss or, in the case of the sixth plate, two bosses. The fifth, fourth, and third plates of Fig. 111 have four bosses, showing a progressive development to this point passing ventrally. The second and first plates are simpler, with fewer spine bosses, retaining at this area something of their youthful simplicity of structure.

In *Arbacia punctulata* (Pl. 24, fig. 111) it is seen that the genital plate has three pores, an abnormal feature. This occurrence of accessory pores is common in this species. In 244 specimens examined from Wood's Holl, Mass., 36 had more than one pore in one or more of the genital plates. The specimen figured has three pores in each genital plate. Two pores were the commonest variation, three pores were not rare however, and one specimen had two pores in two genital plates and three pores, four pores, and seven pores respectively in the other three genital plates. In the 244 specimens examined, 12 had more or less than the typical number of four plates in the periproct. Three or five plates were the commonest variation and are well known, but two specimens showed an increase over this number, one having nine plates in the periproct. In 175 specimens of *Strongylocentrotus drobachiensis* from Massachusetts Bay only two specimens had accessory pores. In one of these specimens there are two pores in the madreporic plate, in the other there are two pores in a genital plate; but as a concurrent variation there are two madreporic plates. In the Palaeozoic genera Rhoechinus, Oligoporus, and Melonites the genital plates have typically more than one pore, varying from two to five; but in Melonites, where best known, usually three or four. The occurrence of accessory pores in Arbacia may be the expression of an atavic tendency, but is more probably to be considered a monstrosity, which, however, is parallel to the normal feature of an ancient but distinct group of Echini.

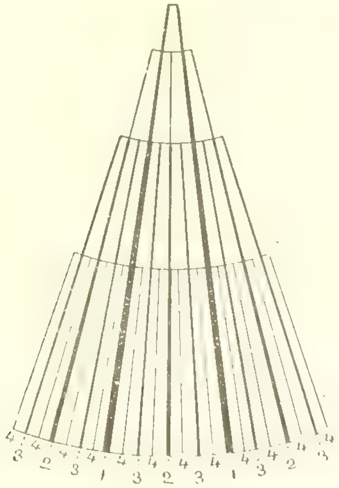
From the above observations on Strongylocentrotus and Arbacia it is seen that there is a distinct ontogenesis of interambulacral plates, in which localized parts we get in a general way a repetition of the ontogenesis which may be traced in following a series of specimens from the young to the adult. As a corollary, it is seen that, passing from the dorsal border of the interambulacrum downward, or ventrally, a progressive series of stages may be traced in progressively older plates of one individual, which are broadly comparable to the stages seen in a progressive series of individuals from the very young to the adult.

Palaeozoic Echini. In studies of *Melonites multiporus* from the Subcarboniferous of St. Louis, Missouri, I have shown ('96) by tabulations of interambulacral areas that these areas may differ in the same individual in regard to the number of columns of plates. In one specimen tabulated (l. c., p. 165) there are eight columns in two areas and nine columns in the other three areas. In another specimen there are eight columns in two areas and nine in two areas, the fifth area being incomplete dorsally. Still a third specimen has seven columns in one area and eight in another. The same feature is shown well in a fine specimen of *Oligoporus missouriensis* Jackson from the Subcarboniferous of Webb City, Missouri. In this specimen, there are five columns of plates in two areas and six in three areas. I have shown ('96) that in the development of Palaeozoic Echini there is a progressive increase in the number of columns of plates until the full number is attained; also, that primitive species have fewer columns than more specialized species. We have, therefore, in this radial differentiation in an adult, an expression of localized radial differentiation, in which some radii are structurally more primitive, while others are more differentiated in the line of evolution of the group.

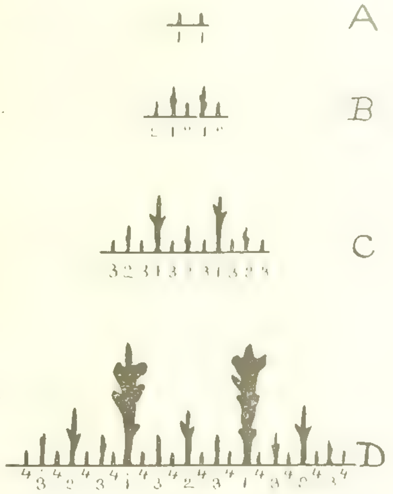
In Echini, the young has a single plate at the ventral border of each interambulacrum (Strongylocentrotus, Fig. 112). This character is a feature of the archaic Bothriocidaris, from the lower Silurian of Russia, as I have pointed out ('96). This single plate in most Echini is lost by the resorption of the ventral border of the corona through the encroachment of the peristome. The primitive character of the single plate is retained in many highly specialized types, as *Lepidechinus rarispinus* Hall and *Pholidocidaris meeki* Jackson, of the Subcarboniferous, also in spatangoids and clypeastroids. These several types are highly specialized in the sum of their characters, but in the localized area about the mouth have retained the embryonic and highly primitive character of single plates at the ventral border of the interambulacra.

In *Lepidechinus rarispinus* Hall, of the Subcarboniferous, the characteristic plates of the interambulacral areas are rounded and imbricating. New plates in Echini are added on the dorsal border of the corona, and at this area the plates of this species are less imbricate and hexagonal. Close to the area of the genital plates they appear to be rhombic in outline. In Melonites and other less specialized Palaeozoic Echini the plates of the interambulacra are hexagonal, and near the dorsal portion of the area are rhombic in outline. Also the plates of these types are not imbricate (except adambulacral plates which extend under adjacent ambulacrals; see Jackson and Jaggar, '96). The evidence, then, is that in *Lepidechinus rarispinus* the young newly formed plates repeat the characters seen normally in the plates of other less specialized types. This relative simplicity of young plates in Lepidechinus first suggested the idea of localized stages in development, and was published essentially as described here (Jackson, '96). Echinoderms are essentially plate-bearing animals. It is probable that in the genesis of newly added plates in many types localized stages may be found which are comparable to stages seen in the young.

SPONDYLUS. Beecher ('98) has pointed out the fact, that in brachiopods and some mollusks, especially pelecypods and conical non-coiled gastropods, localized stages in development may be seen in the multiplication of surface ornamentations through interpolation. Many mollusks present stages of spine development in two directions. (1) The normal series is represented by the succession of spines along a single sector of growth. In the radial plications of a Spondylus or Lima, the earliest and primitive spines are found near the beak, while those on the ventral border of an adult specimen are the latest and most highly developed. (2) By the radial divergence of the ribs and by the interpolation of additional ribs at intervals, as many transverse series of compound spines appear on the periphery as there are primary radii. Hence in a given case, there may be two radii continuing to the beak, then by interpolation there are successively 5, 11, 23, etc., radii, the highest number being found at the periphery (Figs. 12, 13). Moreover, by taking the distal spines on these 23 rows, there result the same [illegible] of spine development as shown in the longitudinal series along any primitive plication (Fig. 13). For example, in Spondylus, Figs. 12 and 13, two radial spinose plications, 1, 1, originate near the umbo. During growth the continuations of these plications diverge, and the



12



13

SPONDYLUS sp.

12. Sector showing diagrammatically the multiplication of radiating lines by interpolation. The first zone A has 2 radii; the second zone B has 5 radii; the third zone C has 11 radii; and the fourth zone D has 23 radii.

13. Profiles of spines produced on the various radii at the four zones as indicated in Fig. 12. A, the spines on the two primary radii of the first zone; B, the spines on the second zone, showing the growth of spines on the [illegible] (1, 1) and the small spines on the newly interpolated radii (2, 2, 2); C, the spines on the radii in the third zone; D, the spines at the bottom of the fourth zone. In zone D the two large compound spines (1, 1) are on the two primary radii. Their development may be traced by following them through A, B, C, to D. The next largest spines (2, 2, 2) [illegible] and represent the stage of spine development attained by the spines on the radii which were interpolated on the second zone B. The next smaller spines (3, 3, 3, 3, 3, 3) are on radii which were introduced in the third zone C. The twelve small spines (4, 4, etc.) are on the radii introduced on the fourth zone D. Thus, there are four stages of spine development shown on the lower margin of the fourth zone, and these correspond to the four stages seen in the series of spines on one of the primary radii running through the four zones. C. E. Beecher, Amer. journ. sci., 1898.

spines become more elaborate, as shown in Fig. 13, zones A–D. The primary plications, with their progressively added spinose modifications, may be taken as the type series. During growth new radial plications (2–4) originate by interpolation. At their inception, zones B, C, D, the spines on new plications resemble the spines of the primary plications at their inception, and during radial growth the spines take on added characters in the same way as did those of the primary plications. This increase by interpolation may be repeated several times in the growth of the individual, with the same result. The localized ontogenesis of radial ornamentation is seen only in the method of development by interpolation. Species in which the radii are all introduced at an early stage in growth (many species of Cardium, Pecten, Lima), or in which radii multiply by regular dichotomy, would show only the longitudinal series (Beecher, '98).

Ammonites. In ammonoid cephalopods septa divide the shell into numerous chambers, and the intersections of these internal partitions with the inner surfaces of the shell, called the sutures, are an important feature in classification. These sutures are often highly complicated, but, as shown by many investigators, the young ammonite has simple sutures. The first formed septum either is simple as in nautiloids, the primitive order of the same class, or in the more specialized ammonites has one or two lobes and saddles. In no ammonites have the first formed sutures dendritic or other plications of lobes and saddles, which are so common in the adult. Simple lobes and saddles in ammonites are characteristic of embryos and primitive types. Senile individuals or degradational types also have simpler sutures than their own adults or the progressive types of their own stock. A greater or less degree of simplicity may, therefore, be accepted as a proof of youth, primitiveness, or degradation.

In studying the individual septa of any of the more specialized ammonites, it is seen that the more complicated lobes and saddles are usually situated on the outer or ventral portion of the septum (Pl. 25, figs. 117–123). Passing from this area inward, or toward the umbilicus, the lobes and saddles become simpler, until close to the umbilicus the simplest lobes and saddles of the septum are found. As stated, simple lobes and saddles are characteristic of the young and of primitive types, and they become progressively more complicated during growth in the individual and the phylum. It appears, then, that in the individual septum of complicated types we have a more or less complete recapitulation of the ontogeny and phylogeny of the type. for as we pass from the umbilicus outward, starting with the relatively simple, there is a progressive complication of lobes and saddles.

Placenticeras placenta. A specimen of *Placenticeras placenta* (Dekay), from the Cretaceous of Dakota, illustrates the relations between the ontogeny of succeeding septa and the evidence of ontogeny as expressed in localized parts of the individual septum. This specimen was kindly loaned me by Prof. Alpheus Hyatt. It is figured on Pl. 25, figs. 117–121. In Fig. 117 the younger portion of this specimen is represented of life size ; at the sections indicated by numbers 118, 119, 120, 121, are situated the septa which are represented enlarged in Figs. 118–121.

A relatively simple septum from one of the younger volutions is shown in Pl. 25, fig. 118. In this septum all the lobes and saddles are simple, but those toward the ventral border are larger and better differentiated. The simple saddles of the whole of this septum are comparable to saddles 7–11 of Fig. 119, saddles 10–11 of Fig. 120, and saddle 11 of Fig. 121.

In the next septum figured (Pl. 25, fig. 119) the first saddle is slightly twice dentate, comparatively complicated. (For brevity in comparison, the saddles and lobes are numbered from 1 upward, instead of external saddle, first lateral saddle, etc., as is frequent in descriptions.) Saddle 2, twice dentate, but simpler. Saddle 3, deeply once dentate, simpler than 2. Saddle 4, once dentate. Saddle 5, once dentate, simpler than saddle 4. Saddle 6, slightly bilobed. Saddles 7–11, entire, like all the saddles of Fig. 118. Lobe 1 has two slight marginal saddles, simple. Lobes 2–4 have each one marginal saddle, progressively decreasing toward the umbilicus. Lobes 5 and 6 have no marginal saddles and are simpler than lobes 3–4. Lobes 7–11 are entire, comparable to all the lobes of Fig. 118.

In the third septum figured (Pl. 25, fig. 120), saddle 1 is twice dentate, the most complex saddle of the septum. Saddles 2–3 are slightly twice dentate, comparable to but more complex than saddle 1 of Fig. 119. Saddle 4 is very slightly twice dentate, comparable to but more complex than saddle 2 of Fig. 119. Saddles 5–7 are distally bilobed, otherwise slightly dentate, comparable to saddles 3–4 of Fig. 119. Saddle 8 is bifid, slightly dentate, comparable to saddle 5 of Fig. 119. Saddle 9 is slightly indented, comparable to saddle 6 of Fig. 119. Saddles 10–11 are entire, comparable to saddles 7–11 of Fig. 119 and all the saddles of Fig. 118. Lobe 1 is uneven in outline, but has two prominences which may apparently be compared to the marginal saddles of lobe 1, Fig. 119. Lobe 2 is irregular, but has two marginal saddles, both slightly dentate. Lobe 3 has one marginal saddle, dentate, and two very slight saddles entire. These entire marginal saddles are comparable to the entire marginal saddles of lobes 1–3, Fig. 119. Lobes 4–8 have slight marginal saddles, comparable to lobes 2–4 of Fig. 119. Lobe 9 has no marginal saddle and is comparable to lobe 5 of Fig. 119. Lobes 10–11 are entire and are comparable to lobes 7–11 of Fig. 119 and all the lobes of Fig. 118.

The fourth septum figured (Pl. 25, fig. 121) is the most complicated of this series. Saddle 1 is deeply twice dentate, the most complex of the septum and more complex than any saddle of Fig. 120. Saddles 2–4 are twice dentate, and comparable to saddle 1 of Fig. 120. Saddles 5–6 are slightly twice dentate and comparable in general to saddles 2–3 of Fig. 120. Saddles 7–8 are lobose, dentate, comparable to saddle 4 of Fig. 120. Saddles 9–10 are bifid, slightly dentate, comparable to saddles 7–8 of Fig. 120. Saddle 11 is entire, comparable to saddles 10–11 of Fig. 120, saddles 7–11 of Fig. 119, and all the saddles of Fig. 118. Lobe 1 has several dentate marginal saddles more than other lobes of its own or preceding septa. Lobes 2–4 have fewer marginal saddles and are generally simpler than lobe 1. Lobe 5 has a simple saddle, and one slightly dentate marginal saddle, comparable to lobe 3 of Fig. 120. Lobes 6–8 have simple marginal saddles, comparable to lobes 5–7 of Fig. 120. Lobes 9–11 have no marginal saddles and are comparable to lobe 9 of Fig. 120 and lobe 5 of Fig. 119. Lobe 12 is entire and is comparable to lobes 10–11 of Fig. 120, lobes 7–11 of Fig. 119, and all the lobes of Fig. 118.

As the relations between the several saddles and lobes in these septa are somewhat complicated, they are tabulated for clearness. In the table it is seen that the simplest conditions exist in the youngest septum, and reading the columns upward it is seen that the later added septa are progressively more complex. Also it is seen that the individual septum decreases in complexity from left to right, as tabulated; or, putting it in another way, the simplest portion of the septum is on the inner or dorsal border, and the septum becomes progressively more complex passing from this area toward the ventral border.

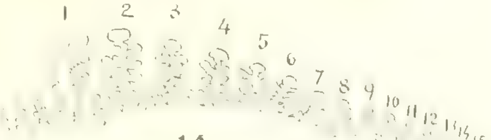
Comparative table of four septa of *Placenticeras placenta* figured on Pl. 25, figs. 117–121.

	Saddles twice dentate.	Saddles once dentate.	Saddles entire.	Lobes with dentate marginal saddles.	Lobes with entire marginal saddles.	Lobes simple with no marginal saddles.	Lobes entire.
Fig. 121 . .	1–8	9–10	11	1–5	6–8	9–11	12
Fig. 120 . .	1–4	5–9	10–11	2–3	1 and 4–8	9	10–11
Fig. 119 . .	1–2	3–6	7–11	0	1–4	5–6	7–11
Fig. 118 . .	0	0	1–11	0	0	0	1–11

Lytoceras and Phylloceras. While the specimen of *Placenticeras placenta* described is especially clear in showing the relations of localized stages in the development of the septa of ammonites, such relations when ascertained are more or less clearly marked in any ammonite and often in Goniatites as well. In a recent paper Prof. James Perrin Smith ('98) shows in a beautiful study of the development of *Lytoceras alamaedense* Smith and *Phylloceras onoense* Stanton, from the upper Cretaceous of California, that in progressively added septa from the protoconch on a similar condition exists to that which I have shown in *Placenticeras placenta*. The lobes and saddles close to the umbilicus repeat the characters seen in the whole septum of early stages, and passing from the umbilicus outward, or ventrally, there is in later septa a localized ontogenesis comparable in general to the ontogenesis presented by successive septa. His paper was received too late to make further use of it than by this note.

A few figures copied from Zittel illustrate the truth of the fact, that the septum carries in itself an epitome of the ontogeny of the septa in the individual and concurrently in the phylum.

Cyclolobus oldhami. In the suture line of *Cyclolobus oldhami* Waagen, one of the simpler Triassic ammonites (Fig. 14), the saddle nearest the umbilicus is almost entire. Passing outward, toward the ventral border, the saddles become progressively more complex, first slightly dentate, then more so, and finally twice dentate in the outermost saddle. Similarly the lobes next the umbilicus are entire; passing outward, slight marginal saddles appear in the eighth lobe. In the fifth and sixth lobes these saddles become roundly indented, and in the first lobe are comparatively complex.



14

Cyclolobus oldhami.

14. Showing suture simple toward umbilicus and progressively more complicated passing to ventral border. After Zittel ('76–'90).

Cladiscites tornatus. In *Cladiscites tornatus* (Bronn), from the European Trias (Pl. 25, fig. 122), the fifth saddle nearest the umbilicus is dentate. The fourth saddle has four short, lateral, branched lobes; passing outward the septum becomes more complex until the first saddle is dendritically branched. The fifth lobe has two slight marginal denticulations; in successive lobes toward the ventral border the marginal saddles increase in number, and become dentately notched.

Phylloceras nilssoni. *Phylloceras nilssoni* (Heb.), from the upper Lias of Europe, has a very complex septum (Pl. 25, fig. 123). The ninth saddle nearest the umbilicus is quite simple, being slightly dentate. In successive saddles, passing outward, the dentations increase in depth and become lobate, until in the third saddle they are slightly twice dentate. The second saddle is still more complex, but the first saddle is somewhat simpler. The ninth lobe nearest the umbilicus is the simplest. In the sixth lobe a small entire marginal saddle appears. In the second lobe there are numerous marginal saddles, part of which are dentate.

Triarthrus beckii. Beecher ('96) from his studies of the appendages of *Triarthrus beckii* Green, of the lower Silurian, has shown that the anterior limbs are long and filiform. Passing posteriorly the limbs are progressively broadened, until those at the posterior portion of the body are relatively very broad and resemble the limbs of phyllopods and also the limbs of many crustacean embryos. As the anterior segments are formed first in the development of the embryo, they have consequently passed through more molts than the posterior segments. To this greater number of molts he ascribes the fact that the anterior appendages are more modified. The posterior appendages, have passed through fewer molts, and have retained the more primitive type of limb. In this regional distribution of primitive and specialized types of limbs it seems that we have another case of localized stages in development.

Vertebral column. In the development of the vertebral column, as I am informed by Dr. Charles Sedgwick Minot, there is evidence of localized stages in development similar to what I have shown in the plates of Echini. In the development of the vertebral column the neck vertebrae are formed first, and from this point additional segments appear both anteriorly and posteriorly. In the caudal vertebrae they originate as did the neck vertebrae and during development pass through ontogenetical stages similar to those which have been previously passed through by the more advanced segments of the column. The subject, however, is one which calls for more exact investigation than has yet been made.

General Conclusions.

As pointed out by Lubbock ('92), in seedling plants the cotyledons are usually more or less strikingly different from the nepionic leaves. They are usually simple in outline, or if lobed, such lobes are usually slight (Eucharidium, Figs. 1–3, page 103); serrations are rare, and cotyledons are usually free from hairs or color markings, although such features may occur in immediately succeeding nepionic growth. This sharp transition from the last embryonic or so-called phylembryonic stage to the nepionic is in accord with what has been observed in many animals at a similar stage. This sharp transition has been shown by Hyatt and others in cephalopods, by Beecher in brachiopods and trilobites, and by myself in pelecypods. In some cases cotyledons during growth may take on nepionic characters, as in Eucharidium, Figs. 1–3, p. 103, and Clarkia. Cotyledons may by acceleration of development acquire some nepionic characters, as noted in serrate spines in cotyledons of the White Pine (Pl. 21, fig. 79a).

Nepionic leaves immediately succeeding the cotyledons are usually simple, even if the adults are compound; or at least simpler than adult leaves, as noted by Lubbock. Amongst known fossil representatives of living plants, these more or less ancient types are usually simpler than modern allies. Nepionic leaves of seedlings, therefore, as representing ontogeny, may be taken in general as repeating in an epitomized form the characters of the adults of ancient fossil allies of the type. Exceptions to this may occur in plants as in animals, where early stages are modified by youthful or larval adaptations. Other exceptions may occur in plants as in animals, which are modified by acceleration of development. An example of acceleration is *Rhus toxicodendron* (Pl. 16, fig. 18) in which the nepionic leaves are as complex as in the adult, though most species of the genus have simple nepionic leaves. Another case is *Ampelopsis tricuspidata* in which the nepionic leaves (Pl. 17, fig. 20) are trifoliolate, whereas the leaves of the adult are unifoliolate. In the allied species, *A. quinquefolia* (Pl. 16, fig. 19), the nepionic leaves are trifoliolate but adult leaves are palmately five foliolate.

Leaves of suckers or branches from the base of the plant, or from the root, frequently repeat the form of nepionic leaves so closely that such may be considered localized reversionary stages. Such reversionary leaves from the base of plants are seen in *Ailanthus glandulosa*, Fig. 14, *Ampelopsis tricuspidata*, Figs. 23, 25, *Negundo aceroides*, Fig. 35, *Fatsia japonica*, Fig. 42, *Tecoma radicans*, *Fraxinus americana*, Fig. 47, *Sassafras sassafras*, *Hicoria ovata*, Fig. 60, *Platanus occidentalis*, Figs. 55, 56, Quercus, several species, Figs. 63, 65, 69, 70, *Pinus rigida*, Fig. 77, *Raphis flabelliformis*, and *Areca lutescens*.

While suckers repeat nepionic characters, they are often highly accelerated in their development, so that only one or two, or a few, leaves at the base are reversionary. Also there may be considerable difference in the degree of reversion in individual suckers, as in the Trumpet Vine, White Ash, and Black Oak, Figs. 69, 70. Suckers may present more primitive characters than the seedling, as *Ailanthus glandulosa*, Fig. 14, in which the first leaves are simpler than the first nepionic leaves of the seedling. As far as observed this is unusual.

Considerable variation often occurs in suckers, as noted in the White Ash, Black Oak, and Ailanthus. While this is more or less confusing in attempting to correlate sucker growth with nepionic and ancestral characters, it is not more so than the variations often found in seedlings, as especially noted in the cases of *Thuya occidentalis* and *Libocedrus decurrens* (p. 119, 122).

Reversionary or localized stages are marked features of abnormal growths, as "birds-nest" growths of the Red Cedar, Fig. 8, p. 117, suckers of the Pitch Pine, Fig. 77. They are frequent in vigorous growths, as terminal shoots of the Red Cedar, Fig. 7, page 117, and Red Maple and *Platanus occidentalis*, Fig. 58. Reversionary features also often occur in feeble or retarded growths, as seen in growths formed late in the season, or on injured branches, Tulip-tree, Ailanthus, *Acer rubrum*, *A. pennsylvanicum*, *A. spicatum*, the White Ash and Red Ash. They may occur in sickly or old age growths, as in the Red Cedar.

It seems that the leaf itself has an ontogenesis repeating more or less fully the ontogeny of the young. In the development of the leaf the distal part is usually formed first, and during growth the proximal parts are progressively added. If this is true, we should expect to find that the distal part of the leaf would be the simplest, most primitive part.

and bear more or less resemblance to the early nepionic leaves of the seedling. Such is found to be the fact in many cases, as Aquilegia, Fig. 17, Liriodendron, Fig. 12, *Ailanthus glandulosa*, Acer, several species, Fig. 29, *Negundo aceroides* frequently, Fig. 36, *Hedera helix*, Fig. 44, *Tecoma radicans*, Fraxinus, several species, Fig. 48, *Sassafras sassafras*, Fig. 51, *Hicoria ovata*, Fig. 61, Cocos, Phoenix, Kentia, Areca, Caryota and many other pinnate palms, Figs. 101, 103, 95, 97.

If the distal end of the leaf repeats nepionic characters, then types which have compound imparipinnate leaves should have a simple nepionic leaf, and such is the case in species observed, the exceptions occurring only when the first leaves by accelerated development are trifoliolate (*Rhus toxicodendron*, Ailanthus). On the same basis, compound paripinnate-leaved types should have compound paripinnate nepionic leaves with two or more leaflets; such is found to be the case in most types (Gleditschia, Fig. 39), but Sesbania, as noted (p. 103), is an exception, having first a simple nepionic leaf.

If the tip of a leaf is the simplest part, then increased complication should take place proximally. This is obviously the case in all imparipinnate leaves. It is markedly the case in *Pteris aquilina* and many other ferns. In some cases the proximal portion of the leaf is the simplest. This is notably the case in *Gymnocladus disicus*, Fig. 37, where lateral divisions are reduced to single leaflets. This simpler or last formed portion is comparable to the simple condition of the sucker and probably of the seedling. To compare with ontogenies of whole organisms: adults or later periods of growth are often simpler than the young in degraded animals, as Ostrea, Baculites, parasitic Crustacea. Adult plants may also be simpler than their own young, *Ampelopsis tricuspidata*, Figs. 20, 22. The tip of the leaf is sometimes the specialized portion, Dionaea, *Cobaea scandens*.

If there is ontogenesis of individual leaves, then any cause which interfered with such development would tend to produce an imperfect, immature, primitive, or reversionary leaf. Such reversionary, more or less isolated leaves are found in Liriodendron, *Ampelopsis quinquefolia*, *Negundo aceroides*, *Gleditschia tricanthos*, *Platanus occidentalis*, *Hicoria ovata*, *Fraxinus americana*, *F. pubescens*, and pinnate palms. In such ontogenies of individual leaves in degraded species we may expect to find localized evidence of ancestral more specialized forms. Such occur in the occasional compound leaves of *Fraxinus anomala*, which species is characterized by simple leaves.

In a word, primitive or reversionary features in adult plants may be looked for in such localized parts as suckers, weak, senile, or abnormal growths, in the distal and proximal parts of leaves, or in unusual individual leaves. How general such localized primitive features or stages in development will prove to be, is uncertain. To prove that they do sometimes exist is all that is attempted here.

New varieties and species in the state of nature are generally supposed to originate by sexual reproduction. The question arises, could such new forms originate from such variations as are seen in localized stages in development of either a progressive or regressive character. It is probable that variations may at least occasionally originate in this manner in the state of nature. Professor Bailey ('96) states that seedlings of varieties which have originated from bud-variation are quite as likely to reproduce the variation as those raised from varieties originated by seed-variation. It is quite possible, therefore, that individuals which differ from the type originated from seed borne on localized branches which differed in the same direction.

In plants, variations in localized areas have been noted in many cases, as in the Tulip-tree, Sassafras, Platanus, Pitch Pine, Red Cedar, etc. In animals, areas of localized variations have been noted in Palaeozoic Echini. Such variations in localized parts as observed are not haphazard and heterogeneous in kind. They are all perfectly definite, being either atavic or progressive variations, and can be correlated with similar characters seen in the young or in fossil representatives, or else in more advanced species of the group to which the animal or plant belongs. Occasional variations cannot be correlated with the ontogeny or phylogeny of the type, such as the split leaves in Libocedrus, Fig. 91. These may properly be considered as monstrosities, comparable to fan-tail pigeons, top-knot fowls, double flowers, cut-leaf birches, etc.

In animals which reproduce asexually by budding, as Hydrozoa and Actinozoa, it seems that the bud may be considered a localized stage (Galaxea, Pl. 24, figs. 106–109). The bud has not the stages seen in early embryonic development from the egg, but repeats in general the later stages seen in such an ontogeny. A bud is not a new individual in the full sense of the word, but is an outgrowth from an older individual by a special localized development.

In animals which, during growth, acquire an addition of similar parts, there is often a strongly marked ontogenesis of such parts, which is parallel to the condition seen in the young or in simpler, less specialized, and ancestral types. Echinoderms, which during growth acquire additional plates, in certain cases show evidence of such localized ontogenesis. Such are the addition of new plates to the stem in the recent crinoids, Metacrinus, Fig. 124, and Pentacrinus, the young newly added plates being comparable to the plates of the whole stem in Jurassic representatives, Fig. 125.

In the Echini (Strongylocentrotus, Figs. 112–116, and Arbacia, Figs. 110–111), new plates are added at the dorsal border of the corona. Such young plates repeat the character seen in all the plates of a very young individual, and are similar to the plates of Cidaris, which is a primitive type in this group. As there is an ontogenesis of the individual plate, so a series of successively older plates presents successive phases of ontogenies; as a result, in passing from the dorsal border of the corona ventrally, a series of stages may be traced which, in general, can be correlated with a similar series in young developing individuals.

In the Palaeozoic echinoid Lepidechinus the new plates added at the dorsal border of the corona are different from the older plates in the same specimen, and present features similar to those seen at the same area in allied less specialized types.

Localized stages in development as represented in budding animals and echinoderm plates, are seen only in the youth of the bud or plate, and during growth are wiped out by changes in the growing part. In the following cases of ornaments of mollusks and septa of cephalopods a different condition exists. The localized stages are permanently fixed in the part and are not capable of modification during further growth of the animal.

Beecher ('98) has pointed out that the spines of radial plications which originate by interpolation in certain brachiopods and mollusks, repeat in their inception and subsequent growth the characters seen in early stages of older plications which originated earlier in the life of the individual; Spondylus, Figs. 12–13, page 133.

In the septa of ammonites that portion of the septum which is nearest the umbilicus is the simplest portion, and repeats more or less fully the condition of the whole septum of the young and of ancestral more primitive types; Placenticeras, Figs. 117–121. As the septum is followed from the umbilicus outward to the ventral border a progressively increasing complication takes place, which is parallel to the progressive complication seen in passing from the young to the adult and concurrently from the geologically earlier to the more recent types. An important feature in this case is the fact that the whole septum is built at one time, representing a single period of growth. Its simpler and more complicated portion, therefore, being built at one time, differ from the simple and more complicated condition of the individual plates of Arbacia and Strongylocentrotus (Pl. 24, figs. 110–116), in which differentiation takes place during the growth of the plate as described.

In the trilobite, *Triarthrus beckii*, localized stages seem to be expressed in the distribution of the ventral appendages, which posteriorly are broad and essentially primitive, while anteriorly they are narrow and specialized (Beecher, '96).

In general, it may be said of localized reversionary stages of adult organisms, that they do not repeat embryonic characters, but earlier or later nepionic or neanic characters, as noted in numerous cases of plants and animals. The chief interest of localized stages in development is the fact, that they call for a comparative study of all parts of the organism, young, adult, and old, and a correlation of these comparisons with the characters in other living and fossil species.

LITERATURE.

Agassiz, Louis.

'63. Methods of study in natural history. Boston, 1863, 319 pp., figs.

Bailey, L. H.

'96. The survival of the unlike. New York, 1896, 515 pp., figs.

Beecher, Charles Emerson.

'96. The morphology of Triarthrus. Amer. journ. sci., ser. 4, vol. 1, p. 251-256, pl. 8.

Beecher, C. E.

'98. The origin and significance of spines, a study in evolution. Amer. journ. sci., ser. 4, vol. 6, 4 pl., figs.

Clark, H. James.

'65. Mind in nature. Boston, 1865, 322 pp., figs.

Deane, Walter.

'96. Notes from my herbarium, V. Bot. gazette, vol. 21, p. 211-214.

Emerson, George B.

'46. Report on the trees and shrubs of Massachusetts. Boston, 1846, 549 pp., 17 pl. Second edition, Boston, 1875, 624 pp., 145 pl.

Holm, Theodor.

'90. Notes on leaves of Liriodendron. Proc. U. S. nat. mus., vol. 13, p. 15-35, pl. 4-9.

Hyatt, Alpheus.

'97. Cycle in the life of the individual (ontogeny), and in the evolution of its own group (phylogeny). Proc. Amer. acad. arts and sciences, vol. 32, p. 209-224.

Jackson, R. T.

'96. Studies of Palaeechinoidea. Bull. geol. soc. Amer., vol. 7, p. 171-254, pl. 2-9.

Jackson, R. T.

'98. Localized stages in growth. Proc. Amer. assoc. adv. sci., vol. 47, p. 359-360.

Jackson, Robert Tracy, and Jaggar, Thomas Augustus, Jr.

'96. Studies of Melonites multiporus. Bull. geol. soc. Amer., vol. 7, p. 135-170, pl.

Lesquereux, Leo.

'91. The flora of the Dakota group. Monogr. U. S. geol. surv., vol. 17, 400 pp., 66 pl.

Lovén, Sven.

'92. Echinologica. Bihang till kongl. svensk. vetenskaps-akad. handl., Stockholm, Bd. 18, afd. 4, 74 pp., 12 pl.

Lubbock, John.

'92. A contribution to our knowledge of seedlings. 2 vols. New York, 1892, 608, 646, 684 figs.

Masters, Maxwell T.

'91. Review of some points in the comparative morphology, anatomy and life-history of the Coniferae. Journ. Linn. soc. London, botany, vol. 27, p. 226-332, figs. 1-29.

Sachs, Julius.

'75. Text-book of botany. Oxford, 1875, 858 pp., 461 figs.

Sargent, Charles Sprague.

'91-'97. The silva of North America. Boston, 1891-97, 11 vols., pl.

Smith, J. Perrin.

'98. The development of Lytoceras and Phylloceras. Proc. Cal. acad. sci., ser. 3, geology, vol. 1, p. 129-160, pl. 16-20.

Strasburger, E., Noll, F., Schenck, H., and Schimper, A. F. W.

'98. A text-book of botany. (Translated by H. C. Porter.) London and New York, 1898, 632 pp., 594 figs.

Thaxter, Roland.

'91. The Connecticut species of Gymnosporangium (cedar apples). Bull. 107, Conn. agric. exper. station, p. 1–6.

Wachsmuth, Charles, and Springer, Frank.

'97. The North American Crinoidea Camerata. Mem. mus. comp. zool., vol. 20-21, 837 pp., 83 pl.

Ward, Lester F.

'87. Types of the Laramie flora. Bull. 37, U. S. geol. surv., 354 pp., 57 pl.

Ward, L. F.

'88. The palaeontologic history of the genus Platanus. Proc. U. S. nat. mus., vol. 11, p. 39–42, pl. 17–23.

Zittel, Karl A.

'76–'90. Handbuch der palaeontologie. München und Leipzig, 1876–90. (Invertebrates and plants, 3 vols., 2616 pp., 2100 figs.).

Explanation of Plates.

C = Cotyledons.

Individual leaves or whorls of leaves are frequently numbered as an aid to description.

PLATE 16.

Liriodendron tulipifera.

Fig. 1. Typical four-lobed leaf of adult. × ¼. P. 94.

Fig. 2. Typical six-lobed leaf of adult, representing by dotted lines the method of dropping out of parts in the formation of a reversionary leaf. A slightly regressive leaf omits two basal lobes a–b, a more regressive leaf omits four basal lobes c–d, a highly regressive leaf is rounded distally e–f. × ¼. P. 95.

Fig. 3. Leaf with eight lobes, an extreme, progressive variation. × ¼. P. 94.

Fig. 4. Reversionary leaf of adult; compare Fig. 2 c–d. × ½. P. 94.

Fig. 5. Early nepionic leaf, with rounded angles and truncate end. × ½. (Holm, '90). P. 95.

Fig. 6. Later nepionic leaf of a seedling showing angles sharpened. × ½. (Holm, '90). P. 95.

Fig. 7. Reversionary leaves on mutilated branch of adult ; compare Fig. 2 a–b, and e–f. × ½. P. 94.

Fig. 8. Seedling showing cotyledons and two nepionic leaves. × ½. P. 93.

Fig. 9. Branch showing progressive variation of an abnormal tree in which Fig. 10 is the typical leaf. Leaf 1 has two slight lateral lobes, leaf 2 has four slight lateral lobes, leaf 3 is regressive, comparable to Fig. 5. × ½. P. 95.

Fig. 10. Typical leaf of a highly reversionary tree, comparable to nepionic leaf Fig. 6. Figs. 9–10 from tree in Arnold arboretum. × ½. P. 95.

Fig. 11. Seedling showing cotyledons and succeeding nepionic leaves, leaf 3 has developed slight lateral lobes. × ½. P. 93.

Fig. 12. Typical six-lobed leaf of adult. × ½. P. 94.

Fig. 13. Reversionary branch showing leaves which in their simplicity approach the condition characteristic of the young ; compare with Fig. 11, also Fig. 2 a–b and e–f. × ½. (Figs. 4, 7, 12, 13 are leaves from one tree. Cultivated, Dorchester, Mass. Figs. 8, 11, seedlings, Milton, Mass.) P. 94.

Ailanthus glandulosa.

Fig. 14. Sucker from root of adult tree, all leaves alternate ; 1–3 simple, 4, trifoliolate, 5–6 quinquefoliolate. Cultivated. × ½. P. 96.

Fig. 15. Seedling showing rounded cotyledons, the first nepionic leaves are opposite, later leaves alternate, all trifoliolate. Leaflets of leaves 3–4 have marginal notches. Cultivated. × ½. P. 96.

Aquilegia canadensis.

Fig. 16. Seedling showing cotyledons and trifoliolate first nepionic leaf. ×1½. P. 93.

Fig. 17. Leaf of adult, the distal end with its major indentations is comparable to the whole [illegible] 16–17 cultivated, Dorchester, Mass. P. 93.

Rhus toxicodendron.

Fig. 18. Seedling showing cotyledons and nepionic leaves, the first two opposite, succeeding leaves alternate, all trifoliolate with lobes in the proximal leaflets. West Chop, Martha's Vineyard, Mass. ×½. P. 97.

Ampelopsis quinquefolia.

Fig. 19. Seedling showing ovate cotyledons and three nepionic leaves, all alternate, 1, 2, trifoliolate, but leaf 3 is quinquefoliolate, like the adult. West Chop, Martha's Vineyard, Mass. ×½. P. 97.

Figs. 16–17 drawn by Mr. J. H. Emerton; others by the author.

PLATE 17.

Ampelopsis tricuspidata.

Fig. 20. Seedling showing broadly ovate cotyledons and alternate, trifoliolate, nepionic leaves. ×1. P. 98.

Fig. 21. Tip of an older seedling. Leaf 1 is trifoliolate, as are all the leaves proximally in this specimen. Leaf 2 has a lateral leaflet on one side. Later leaves are all unifoliolate, dentate. ×½. Figs. 20-21, Shady Hill nursery. P. 98.

Fig. 22. Typical unifoliolate, trilobed leaf from old wood of adult. Compare Fig. 25b. ×½. P. 98.

Fig. 23. Trifoliolate leaf from base or nepionic area of adult vine. Compare Figs. 20 and 25a. ×½. P. 98.

Fig. 24. Unifoliolate, dentate leaves from wood of current season's growth. Compare Figs. 21 and 25c. ×½. Figs. 22–24 all from one vine, cultivated. Vineyard Haven, Mass. P. 98.

Fig. 25. Diagram showing distribution of types of leaves in adult vine raised from seed. Area a, near base of vine, leaves trifoliolate; area b, old wood, leaves unifoliolate, trilobed; area c, wood of current season's growth, leaves unifoliolate, cordate, dentate. Compare with Figs. 20–24. P. 98.

Acer rubrum.

Fig. 26. Tip of branch of adult, with young leaves, all elongate, trilobed, especially leaf 2. ×½. P. 99.

Fig. 27. Sucker from base of adult tree. Leaves, especially 2, elongate, trilobed. ×½. Figs. 26–27. West Chop, Martha's Vineyard, Mass. P. 99.

Fig. 28. Seedling, cotyledons elongate, nepionic leaves, 1 nearly ovate, dentate, 2 elongate, trilobed. Jackson, N. H. ×1. P. 99.

Fig. 29. End of branch of adult showing, 1 typical leaf of species, and 3 a, b elongate trilobed leaves. West Chop, Martha's Vineyard, Mass. ×½. P. 99.

Acer oblongum.

Fig. 30. Species having elongate, entire leaves, the veining is similar to that of the Red Maple, Fig. 29. ×½. Province of Hupeh, China. ×½. P. 100.

Acer carpinifolium.

Fig. 31. Species having leaves with slightly serrate margin, but no lobes. Nikko, Japan. ×½. P. 100.

Acer crataegifolium.

Fig. 32. Species having leaves with slightly developed lobes, compare the two leaves of this figure with leaves [illegible] Fig. 28. Nikko, Japan. ×½. P. 100.

ACER TARTARICUM VAR. GINNALE.

Fig. 33. The proximal pair of leaves entire, very slightly dentate, the next pair with well developed lobes, compare with leaves 2, Fig. 28. Jesso, Japan. × ½. Figures 30–33 from specimens in herbarium of Arnold arboretum. P. 101.

Figs. 30–33 drawn by Mr. J. H. Emerton; others by the author.

PLATE 18.

ACER PLATANOIDES.

Fig. 34. Sucker from stump of adult, showing trilobed leaves. Cultivated. × ½. P. 100.

NEGUNDO ACEROIDES.

Fig. 35. Sucker from base of adult with a simple, trilobed leaf followed by a trifoliolate leaf (as leaves are opposite in this species the mates of the two leaves figured must be considered absent from accident or repression). Cultivated. × ½. P. 102.

Fig. 36. Typical leaf of adult. Cultivated. Reduced. P. 102.

GYMNOCLADUS DISICUS.

Fig. 37. Typical but small leaf of adult, twice pinnate distally, once pinnate proximally. Much reduced. P. 102 and 140.

Fig. 38. Sucker from root of same tree as Fig. 37, leaf once pinnate. Cultivated. × ½. P. 102.

GLEDITSCHIA TRIACANTHOS.

Fig. 39. Seedling showing the cotyledons which are oval, auricled at the base embracing the stem, the nepionic leaves are alternate, paripinnate, with many leaflets. Cultivated. × ½. P. 102.

FATSIA JAPONICA.

Fig. 40. Small but typical leaf of adult, palmately deeply cleft. Cultivated. × ¼. P. 104.

Fig. 41. Seedling showing obovate cotyledons, and nepionic leaves 1 ovate, 2 subcordate, 3 trilobed, all finely serrate. Cultivated. × ½. P. 104.

Fig. 42. Sucker from the base of an adult raised from seed, leaf 1 trilobed, 2 subcordate, both finely serrate. Compare Fig. 41. Cultivated. × ½. P. 104.

HEDERA HELIX.

Fig. 43. Seedling showing cotyledons ovate, nepionic leaves alternate, 1, subcordate with a slight lobe on one side; 2, subcordate, nearly triangular; 3, five-lobed; 4 (younger), weakly trilobed; 5, nearly triangular; compare with leaf 2. Florence, Italy. × ½. P. 104.

Fig. 44. Branch of adult vine, leaf 1, five-lobed; 5 (younger), weakly five-lobed; 6–8, broadly trilobed; compare with Fig. 43. Cultivated. × ½. P. 105.

FRAXINUS AMERICANA.

Fig. 45. Seedling showing cotyledons elongate, distally blunt, and nepionic leaves, simple, opposite, elongate-ovate, petiolate. × ¼. P. 105.

Fig. 46. Tip of older seedling. First nepionic leaves (not shown) all simple, next leaves trifoliolate, lateral leaflets sessile, terminal leaflet petiolulate. × ¼. P. 106.

Fig. 47. Sucker from root near the base of an adult tree. First leaves alternate, simple, petiolate, oval, distally acuminate, terminal leaves opposite, trifoliolate, lateral leaflets sessile, terminal leaflet petiolulate, all leaves except 1 serrate. Compare Figs. 45–46. × ¼. Figs. 45–47, Milton, Mass. P. 106.

Fig. 48. Typical leaf of adult, lateral and terminal leaflets petiolulate. Compare with Figs. 46, 47. [illegible] '75) reproduced by permission. Reduced. P. 106.

Figs. 34–48 drawn by the author.

PLATE 19.

SASSAFRAS SASSAFRAS.

Fig. 49. Seedling showing fruit adherent, nepionic leaves alternate, elongate-oval. Leaf 6 has slight marginal depressions. Shady Hill nurseries, Bedford, Mass. ×½. P. 107.

Fig. 50. Tip of an older seedling, all proximal leaves (not shown) oval, terminal leaves two or three lobed. West Chop, Martha's Vineyard, Mass. ×½. P. 108.

Fig. 51. Small but entire branchlet of adult, first four leaves entire, oval. Succeeding leaves three-lobed, compare Figs. 49–50. West Chop, Martha's Vineyard, Mass. ×½. P. 108.

MYRICA CERIFERA.

Fig. 52. Seedling showing broad, spathulate, distally emarginate cotyledons. The first nepionic leaves are spathulate tridentate, without petioles, in later nepionic leaves more dentations and petioles develop progressively. ×¾. P. 113.

Fig. 52a. Enlargement of cotyledons and first nepionic leaves. ×3. Arnold arboretum. P. 113.

Fig. 53. Typical leaves of adult, oval, petiolate, distally dentate. Compare with young leaves of Fig. 52. Cohasset, Mass. ×½. P. 113.

PLATANUS ORIENTALIS.

Fig. 54. Seedling showing strap-shaped cotyledons, and nepionic leaves which are elongate, cuneate, distally tridentate. In these leaves the blade extends to the base of the leaf, no petiole having developed. (Lubbock, '92.) Reproduced by the courtesy of Messrs. D. Appleton & Co. ×1. P. 109.

PLATANUS OCCIDENTALIS.

Fig. 55. Sucker from the base of an adult tree, leaves elongate, cuneate, distally dentate, blade extending nearly to the base of the petiole. Compare with Fig. 54. ×1. P. 109.

Fig. 56. Another sucker from the base of an adult tree. Leaves elongate, trifid to trilobed distally, blades extending far down toward base of petiole. ×½. P. 109.

Fig. 57. Typical leaf of adult, five-lobed, marginally dentate, blade extends only a short distance down the petiole forming an obtuse angle proximally. ×½. P. 110.

Fig. 58. Vigorous leaf from the upper part of a sucker (several feet from the ground), five-lobed, highly dentate marginally with a prominent basal lobe which stands out free from the petiole, Fig 58a, so that the leaf is perfoliolate. ×½. P. 109.

Fig. 58b. Stipules forming an encircling ruffle about the base of the petiole of leaf Fig. 58. ×½. Figs. 55–58 all from one tree. Milton, Mass. P. 109.

Figs. 52–53 drawn by Mr. J. H. Emerton; others by the author.

PLATE 20.

HICORIA OVATA.

Fig. 59. Seedling showing nut resting on the ground (dotted line), nepionic leaves 1–3 simple, ovate. Leaf 4 abnormal with one lateral leaflet. Leaves 5–6 trifoliolate. ×½. P. 110

Fig. 60. Sucker from the base of an adult tree. Leaves 4–5 simple, ovate; leaves 6–7 abnormal, with one lateral leaflet; leaves 9–10 trifoliolate. ×½. P. 110.

Fig. 61. Tip of branch of an adult, showing 1, typical leaf of the species; 2, trifoliolate leaf occurring typically at the end of branches. Compare with Figs. 59–60. ×½. Figs. 59–61, Milton, Mass. P. 110.

QUERCUS ALBA.

Fig. 62. Seedling showing cotyledons enclosed in the acorn and succeeding nepionic leaves, 1, elongate, oval, very slightly sinuate; leaves 2–3 slightly lobed. ×½. P. 111.

Fig. 63. Sucker from the base of an adult tree. Leaf 1 nearly entire; later leaves progressively more lobate. ×½ P. 111.

Fig. 64. Typical leaf of adult. ×½. P. 111.

QUERCUS MINOR.

Fig. 65. Sucker from the base of an adult tree, leaves nearly entire, 1 oval, 2 obovate, slightly lobed. ×½. Pl. 111.

Fig. 66. Typical leaf of adult. ×¼. P. 111.

QUERCUS TINCTORIA, OR Q. COCCINEA.

Fig. 67. Seedling, cotyledons enclosed in acorn (dissected out in diagram). Nepionic leaves 1–3 oval, with a small spine at end of the midrib; leaf 4, slightly undulous with spines at the tips of the principal veins. ×½. P. 111.

Fig. 68. Seedling showing the petioles of the cotyledons extending from the acorn as in other figures. First leaves small, entire; leaves 3–4 much larger, undulous, with spines at tips of principal veins. ×½. P. 111.

QUERCUS TINCTORIA.

Fig. 69. Sucker from the base of an adult. First leaf oval with a spine at the tip of the midrib, later leaves undulous, or lobed. Compare with Figs. 67–68. × ½. P. 112.

Fig. 70. Suckers from the base of an adult. First leaf undulous with spines at tips of leading veins; next leaf more lobed. Compare with Fig. 68. ×½ P. 112.

Fig. 71. Typical leaf of adult. ×¼. Figures 62–71 from West Chop, Martha's Vineyard, Mass. P. 112.

Figs. 59–71 drawn by the author.

PLATE 21.

PINUS RIGIDA.

Fig. 72. Seedling showing cotyledons bound together distally by the remains of the seed coats, and nepionic leaves protruding thickly from the short stem. ×1½. P. 113.

Fig. 73. A little older seedling showing cotyledons free distally, smooth, triangular in section (Fig. 73, b). Nepionic leaves thickly clothing the stem, the individual leaves, Fig. 73a, flat on the inner side, curved on the outer side with two marginal rows of serrate spines. ×½. P. 113.

Fig. 74. Older seedling showing the nepionic primary leaves at the base, succeeded by clusters of needles in the axils of primary leaves. ×⅔. P. 114.

Fig. 74a. Cluster of needles in the axil of a primary leaf from the tip of Fig. 74. ×1. Fig. 74b. Section of cluster at the base where surrounded by a sheath. Fig. 74c. Fragment of one of cluster leaves showing form and the rows of minute saw-like teeth on the three angular ridges. Enlarged. P. 114.

Fig. 75. Cluster of leaves in the axil of a scale from an older seedling, which in this feature has attained adult characters. ×⅔. P. 114.

Fig. 76. Sucker from a stump showing reversionary primary leaves with bundles in their axils as in the later growth of

a seedling (see Fig. 74). [illegible]. Fig. a, section of primary leaf showing the form and the spines on the two edges. Compare with Figs. 73–74. P. 114

Fig. 77. Another sucker from the stump, very vigorous and showing only reversionary primary leaves. Compare Figs. 73–76. ×⅔. Figs. 72–77, West Chop, Martha's Vineyard, Mass. P. 114.

PINUS STROBUS.

Fig. 78. Seedling showing cotyledons bound together distally by the seed coats. ×2. P. 115.

Fig. 79. An older seedling showing cotyledons expanded and succeeding primary leaves. ×2. Cotyledons bear spines on the three angles Fig. a, as in adult leaves. Primary leaves bear spines on two edges, Fig. b, as in *Pinus rigida*, Fig. 73a. P. 115

Fig. 80. Still older seedling showing cotyledons and succeeding primary leaves. ×2. Figs. 78–80, Arnold arboretum. P. 115.

Fig. 81. Older seedling, showing nepionic leaves at the base and bundles of 5 leaves in the axils of the primary leaves at the top. (Part of the bundles are omitted for the sake of clearness.) [illegible]. P. 115.

Fig. 81a. One of the leaf bundles and subtending primary leaf. ×1. Fig. 81b, section of bundle in the plane of the sheath showing the angular form of leaves at that area. Fig. 81c, fragment of leaf showing form and three rows of minute spines on angles, much enlarged. Shady Hill nurseries, Bedford, Mass. P. 116.

LARIX OCCIDENTALIS.

Fig. 82. Seedling showing cotyledons and succeeding nepionic primary leaves. ×⅔. Kindness of Mr. C. E. Faxon. P. 116

LARIX EUROPAEA.

Fig. 83. Fragment of adult branch showing leaves in bundles on old wood, and primary leaves only on current season's growth. Compare with Fig. 82. Cultivated. ×⅔. P. 116.

Figs. 78–80 drawn by Mr. J. H. Emerton; others by the author.

PLATE 22.

THUYA OCCIDENTALIS.

Fig. 84. Seedling showing cotyledons, c, and succeeding nepionic leaves. 1, 2, are in whorls of four leaves, succeeded by whorls of two leaves throughout succeeding growth. Primary leaves extend to top of the stem. Leaves on lateral branches are appressed, distally pointed (enlarged ×4 in Fig. 84b). Beedes, Adirondacks, N. Y. ×2. P. 119.

Fig. 84a. Plan of arrangement of cotyledons and first whorl of nepionic leaves of Fig. 84. P. 119.

Fig. 85. Branchlet of adult showing characteristic leaves which are more abbreviated and appressed than in the young, as shown in Fig. 84b. Beedes, Adirondacks, N. Y. ×4. P. 120.

Fig. 86. Seedling showing cotyledons and succeeding nepionic leaves. First nepionic leaves 1, a whorl of two leaves. Second whorl, 2, four leaves; succeeded by whorls of three leaves (an aberrant character in this species) on the main stem. On the branch the leaves are in whorls of twos, and are soon abbreviated, appressed, as in the branch of Fig. 84. Cultivated. Andover, Mass. ×2. P. 120.

Fig. 86a. Plan of cotyledons c, and first three whorls of nepionic leaves 1, 2, 3, of Fig. 86. P. 120.

THUYA GIGANTEA.

Fig. 87. Seedling showing cotyledons and succeeding growth. First nepionic leaves 1, in a whorl of two leaves, second whorl 2, and succeeding whorls composed of four leaves until near top of main stem, where some leaves are in whorls of twos. On branches, leaves are in whorls of twos; proximally, the leaves are elongate primaries, but soon the leaves are

shortened, appressed. The branches differ from those of *T. occidentalis*, Fig. 84, in the angle of divergence, and the appressed leaves are narrower, more acuminate than in the seedling of that species. ×2. Arnold arboretum, from seed collected at Ashford, Washington. P. 121.

Fig. 87a. Plan of cotyledons c, and first two whorls of nepionic leaves 1, 2. P. 121.

Libocedrus decurrens.

Fig. 88. Typical seedling, showing cotyledons c, and nepionic leaves which are all primaries. First whorl 1 consists of two leaves, second 2 and succeeding whorls all consist of four leaves. ×2. Compare Fig. 9, P. 122. P. 121.

Fig. 89. Older typical seedling, cotyledons and succeeding leaves arranged as in Fig. 88. On branches and top of main stem the leaves become broadened, shortened and approach the character of adult leaves. ×2. Compare Fig. 9, P. 122. P. 121.

Fig. 89a. Tip of branch of Fig. 89 enlarged showing leaves relatively broad and appressed as compared with primary leaves, all in four-leaved whorls ×4. P. 122.

Fig. 90. Character leaves of adult, broader, more appressed, and distally blunter than in the young (Fig. 89a), leaves all in whorls of four. From herbarium specimen, Arnold arboretum. ×4. P. 122.

Fig. 91. Seedling, aberrant in that the first whorl of nepionic leaves 1, consists of four leaves, which are proximally fused in two pairs as shown enlarged in Fig. 91a. ×2. Compare Fig. 11, P. 122. P. 122.

Fig. 92. Seedling aberrant in that the primary leaves succeeding the first whorl 1, are in whorls of twos instead of fours as is the normal condition. ×2. Compare Fig. 10, P. 122. All *Libocedrus decurrens* seedlings from Arnold arboretum, from seed collected in Oregon. P. 123.

Figs. 84–92 drawn by Mr. J. H. Emerton.

PLATE 23.

Latania commersonii.

Fig. 93. Leaf of young plant showing broadening and distal splitting from mechanical tension. Compare with seed-leaf Fig. 94. × about ⅓. P. 124.

Fig. 93a. Lower side of leaf Fig. 93, showing rachis. P. 124.

Fig. 94. Seedling showing elongate, lanceolate nepionic leaf with an elongate rachis. Reduced. P. 124.

Chrysalidocarpus lutescens.

Fig. 95. Seedling, leaves 1 and 2, simple, distally deeply cleft; leaf 3 compound, but the distal tip resembles the whole of the simple leaves 1, 2. Reduced. Compare with Figs. 96, 98. P. 126.

Kentia balmoreana.

Fig. 96. Seedling with seed in place and early nepionic leaf. This leaf is of the cleft type; but is distally fused. Compare Fig. 98 and leaf 1 of Fig. 95. Reduced. P. 126.

Caryota cumingii.

Fig. 97. Seedling, early compound, pinnate leaf, deeply cleft, the leaflets distally irregularly truncate. Reduced. P. 125.

Fig. 98. Seedling, simple leaf, younger than Fig. 97, distally very deeply cleft. Compare Fig. 96, and leaf 1, Fig. 95. Reduced. P. 125.

Diplothemium maritimum.

Fig. 99. Developing leaf of a young seedling showing adhesion of the pinnae by their distal borders. Compare Figs. 96 and 101. Reduced. P. 125.

Phoenix canariensis.

Fig. 100. Seedling with seed in place, showing elongate character of the stage, [illegible] compare with older Phoenix, Fig. 103. ×½. P. 124.

Cocos weddelliana.

Fig. 101. Pinnate leaf of a young seedling, the terminal leaflet resembles the whole of [illegible] compare Fig. 102. The lateral pinnae near the tip of leaf cling to one another and to the distal leaflet. Reduced. P. 124.

Fig. 102. Simple nepionic leaf of a young seedling, leaf is entire, elongate with elongate rachis. Reduced. P. 124.

Phoenix rupicola.

Fig. 103. Seedling showing simple leaf 1, succeeded by compound pinnate leaves 2, 3. The [illegible] of leaves 2 and 3 are similar to the whole of leaf 1. The lateral pinnae of 2 and 3 near the end cling to terminal leaflet. × about ½. P. 124.

Fig. 103a. Reverse side of leaf 1 of Fig. 103, showing elongate rachis. P. 124.

Corypha australis

Fig. 104. Simple leaf of young seedling, showing ovate form and elongate rachis. Reduced. Fig. a, reverse side of leaf showing rachis more distinctly. Reduced. P. 124.

Pteris aquilina.

Fig. 105. Young plant; the frond is entire distally, becoming progressively more divided proximally. Dotted line represents the surface of soil. West Chop, Martha's Vineyard, Mass. Slightly enlarged. P. 126.

Figures 93–104 from plants in cultivation.

Fig. 105 drawn by the author; others by Mr. J. H. Emerton.

PLATE 24.

Galaxea caespitosa.

Fig. 106. Young bud from coenenchyma of adult colony, showing only six septa. ×12. P. 127.

Fig. 107. Older bud. The first six septa have grown and six additional septa have appeared. ×12. P. 127.

Fig. 108. Still older bud, all the twelve septa of Fig. 107 have grown and the six oldest are represented by costae externally. ×8. P. 127.

Fig. 109. Fully grown zooid, the twelve septa of Figs. 106–108 have grown and fused centrally. Additional tertiary septa occur between the primary and secondary septa. These tertiary septa are in the condition of development represented by the primary septa of Fig. 106 and the secondary septa of Fig. 108. ×8. All the polyps, Figs. 106–109, are from a single large specimen in the collection of the Bost. soc. nat. hist. P. 127.

Arbacia punctulata.

Fig. 110. Interambulacrum of a young specimen (23 mm. in diameter) having eleven plates in the columns. Plate 11 has no spine boss, plate 10 has one, and plate 6 has two bosses. Compare with plates 11, 10, 6, of Fig. 111. Wood's Holl, Mass. ×3. p. 130.

Fig. 111. Interambulacrum of adult specimen (measuring 45 mm. in diameter), having 14 plates in columns. Plate 14 is smooth, plate 13 has one spine boss, plate 10 has two spine bosses. Compare with plates of Fig. 110. Wood's Holl, Mass. ×3. P. 130.

STRONGYLOCENTROTUS DROBACHIENSIS.

Fig. 112. Interambulacrum of a very young specimen (measuring 1.2 mm. in diameter), showing plates of interambulacrum from ventral side, the single ventral plate 1, and succeeding plates 2, 3, have each one spine boss. (Lovén, '92.) × about 55. P. 129.

Fig. 113. Interambulacrum of a little older specimen (measuring 2.2 mm. in diameter) showing a partial resorption of single ventral plate 1, and two spine bosses on the second plate of the right hand column. (Lovén, '92.) × about 32. P. 129.

Fig. 114. Interambulacrum of a young specimen (measuring 7 mm. in diameter) showing 11 plates in interambulacral columns. Compare plate 11 with all plates of Fig. 112, plates 11 and 16 of Fig. 115 and plates 11 and 21 of Fig. 116. ×6. P. 129.

Fig. 115. Interambulacrum of an older specimen (measuring 25 mm. in diameter), showing 16 plates in interambulacral columns. The youngest plate 16 of the left-hand column, resembles all the plates of Fig. 112, also plate 11 of Fig. 114 and plates 21–22 of Fig. 116. Compare also with plate 16 of Fig. 116. ×6. P. 129.

Fig. 116. Interambulacrum of an adult specimen (measuring 52 mm. in diameter) showing 22 plates in interambulacral columns. The youngest plates, 21 and 22, have a single spine boss and are comparable to all the plates of Fig. 112, plate 11 of Fig. 114, and plate 16 of Fig. 115. ×3. P. 129.

Fig. 116a. The fifteenth plate of the left hand column of Fig. 116, enlarged to show full detail of surface ornamentation. ×6. Figs. 114–116, Massachusetts Bay. P. 130.

Figs. 106–116 drawn by Mr. J. H. Emerton.

PLATE 25.

PLACENTICERAS PLACENTA.

Fig. 117. The immature portion of a large specimen. The lines 118, 119, 120, 121 show the positions of the septal sutures represented in Figs. 118–121. ×1. Cretaceous, Dakota. Coll. Prof. A. Hyatt. P. 134.

Fig. 118. A comparatively early septum, all saddles and lobes entire. Enlarged. P. 134.

Fig. 119. A later septum more complicated than Fig. 118. Lobes and saddles near the umbilicus are similar to all the lobes and saddles of Fig. 118. Enlarged. P. 135.

Fig. 120. A later septum still more complicated. The saddles and lobes near the umbilicus are like all the saddles and lobes of Fig. 118. For other comparisons, see text. Enlarged. P. 135.

Fig. 121. A later septum more complicated than Fig. 120. The lobes and saddles close to the umbilicus are simple like all the lobes and saddles of Fig. 118. For other comparisons, see text. Enlarged. P. 135.

CLADISCITES TORNATUS.

Fig. 122. Showing septal suture simple toward umbilicus, complicated on ventral portion. Triassic, Hallstadt. (Zittel, '76–'90.) P. 137.

PHYLLOCERAS NILSSONI.

Fig. 123. Showing suture line simple toward umbilicus and progressively more complicated toward ventral border. Jurassic. (Zittel, '76–'90.) P. 137.

METACRINUS ROTUNDUS.

Fig. 124. Showing dense association of cirrhi and pentagonal form of stem near the calyx. Fig. a, section of same (drawn from surface study). ×1½. P. 127.

Fig. 124a. The same specimen, portion of stem at a considerable distance from calyx, showing widely spaced cirrhi and nearly round form of stem. At the base of figure the plates of the stem are indicated. Fig. a, section of stem (drawn from surface study). ×1½. Fig. 124, Japan, Coll. Bost. soc. nat. hist. P. 127.

PENTACRINUS (EXTRACRINUS) BRIAREUS.

Fig. 125. Showing dense association of cirrhi and pentagonal form of stem. [illegible] throughout the length of the stem in this species. ×1½. Jurassic. Enlarged. (Zittel, '76-'90.) P. 128.

Fig. 125a. Section of stem. (Zittel, '76-'90.) P. 128.

PENTACRINUS BASALTIFORMIS.

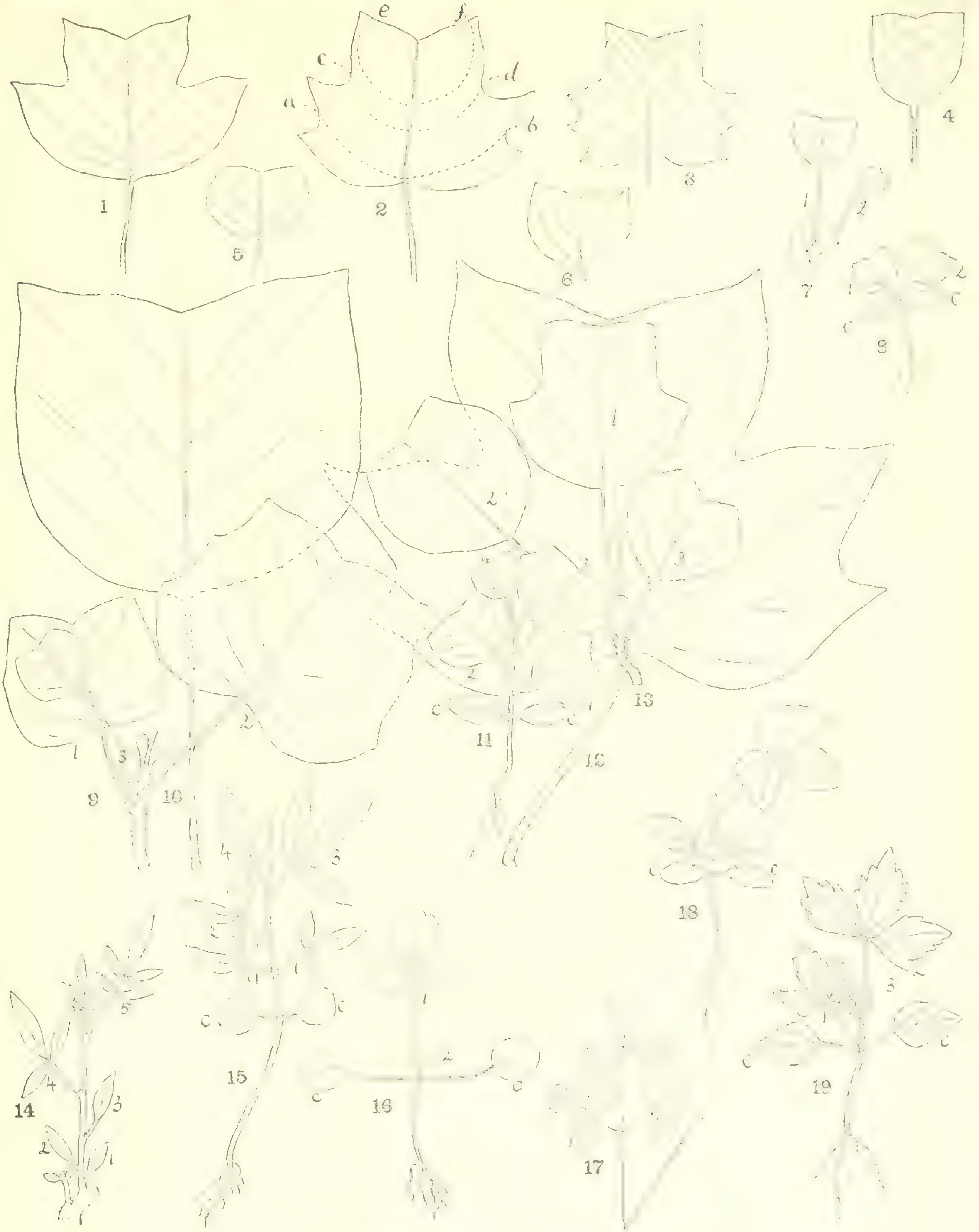
Fig. 126. Showing strongly pentagonal form of stem. Jurassic. (Zittel, '76-'90.) P. 128.

PLATYCRINUS SYMMETRICUS.

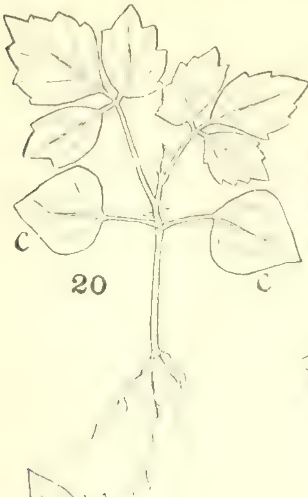
Fig. 127. Showing circular form of young plates of stem close to calyx and the change to oval form of plate in the older part of stem. Subcarboniferous, Iowa. ×1½. (Wachsmuth and Springer, '97.) Fig. a, Section of stem close to calyx, Fig. b, section further down the stem drawn from surface study. ×1½. P. 128.

Figs. 117–127 drawn by Mr. J. H. Emerton.

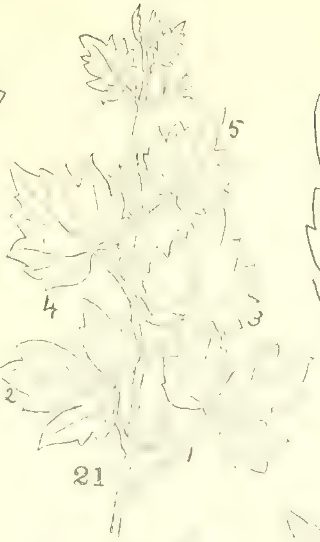
Printed, April, 1899.



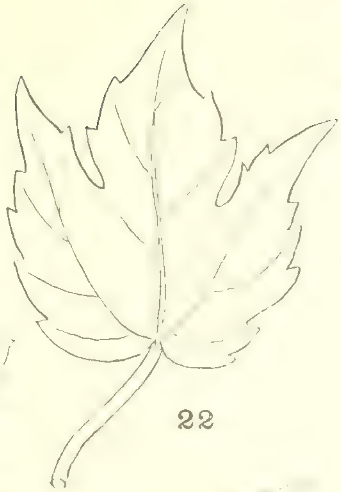
JACKSON, LOCALIZED STAGES.



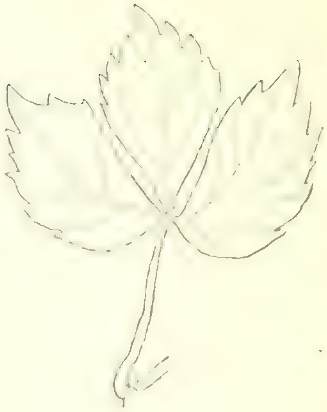
20



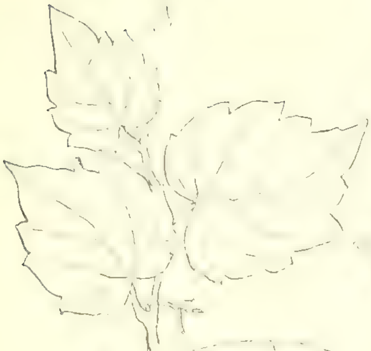
21



22



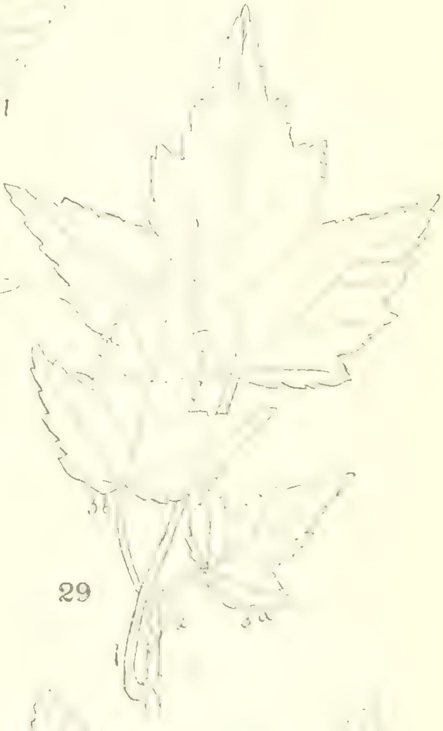
23



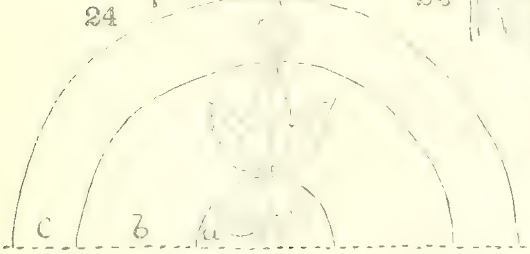
24

26

28

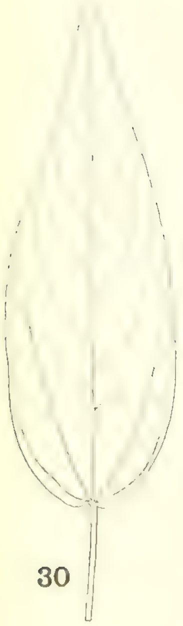


29



25

27



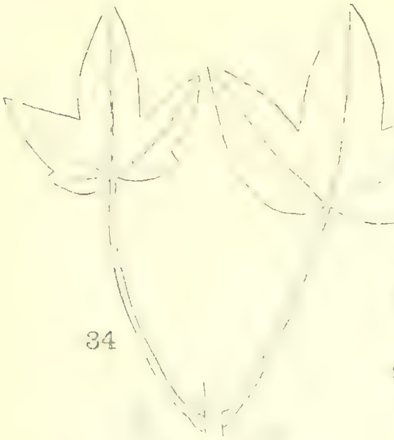
30

31

32

33

Jackson, Localized Stages.

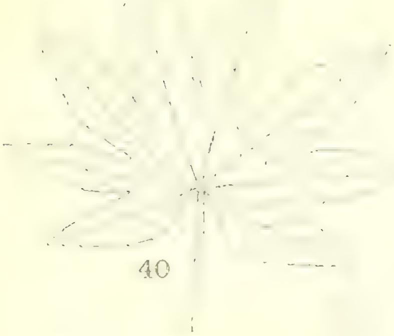


34

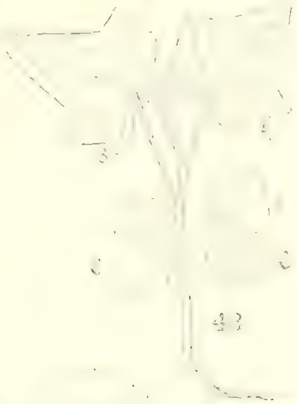
35

36

39

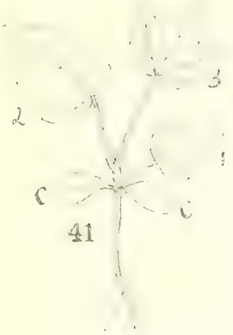


40



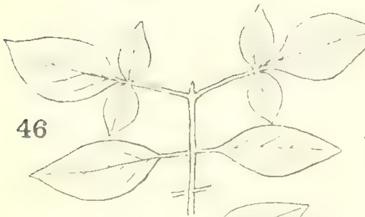
43

44

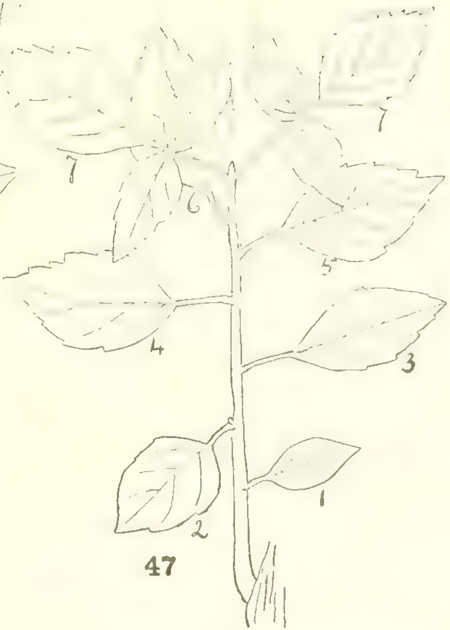


41

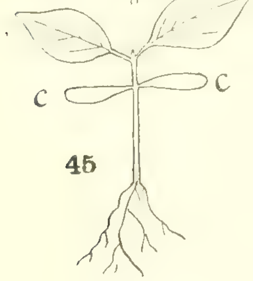
42



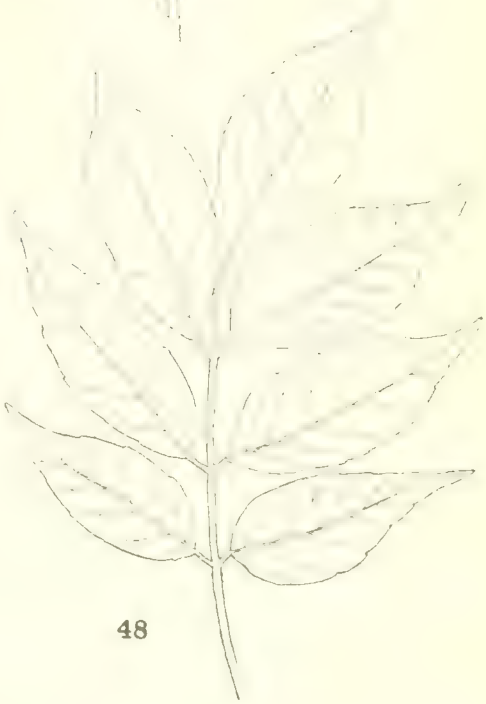
46



47

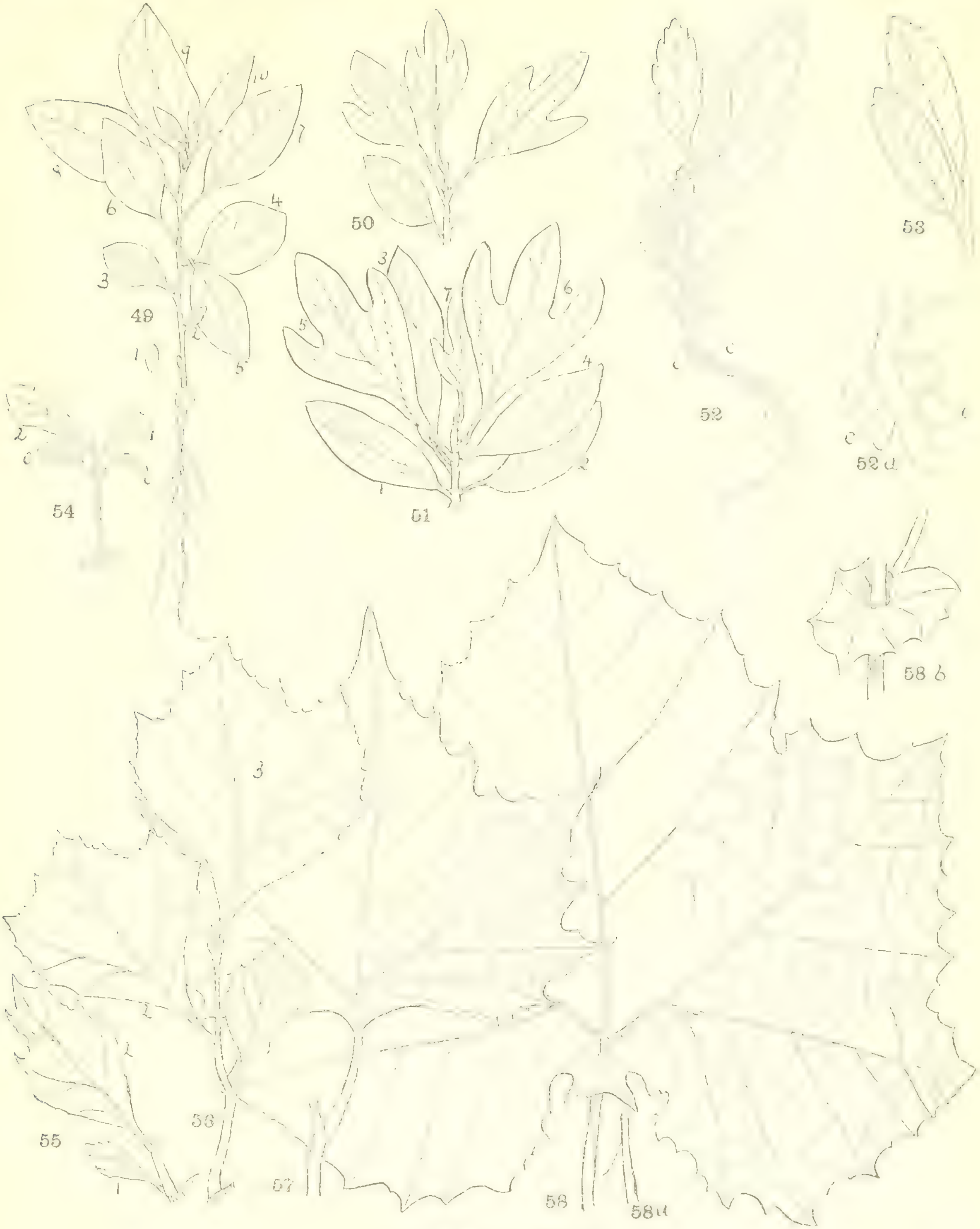


45

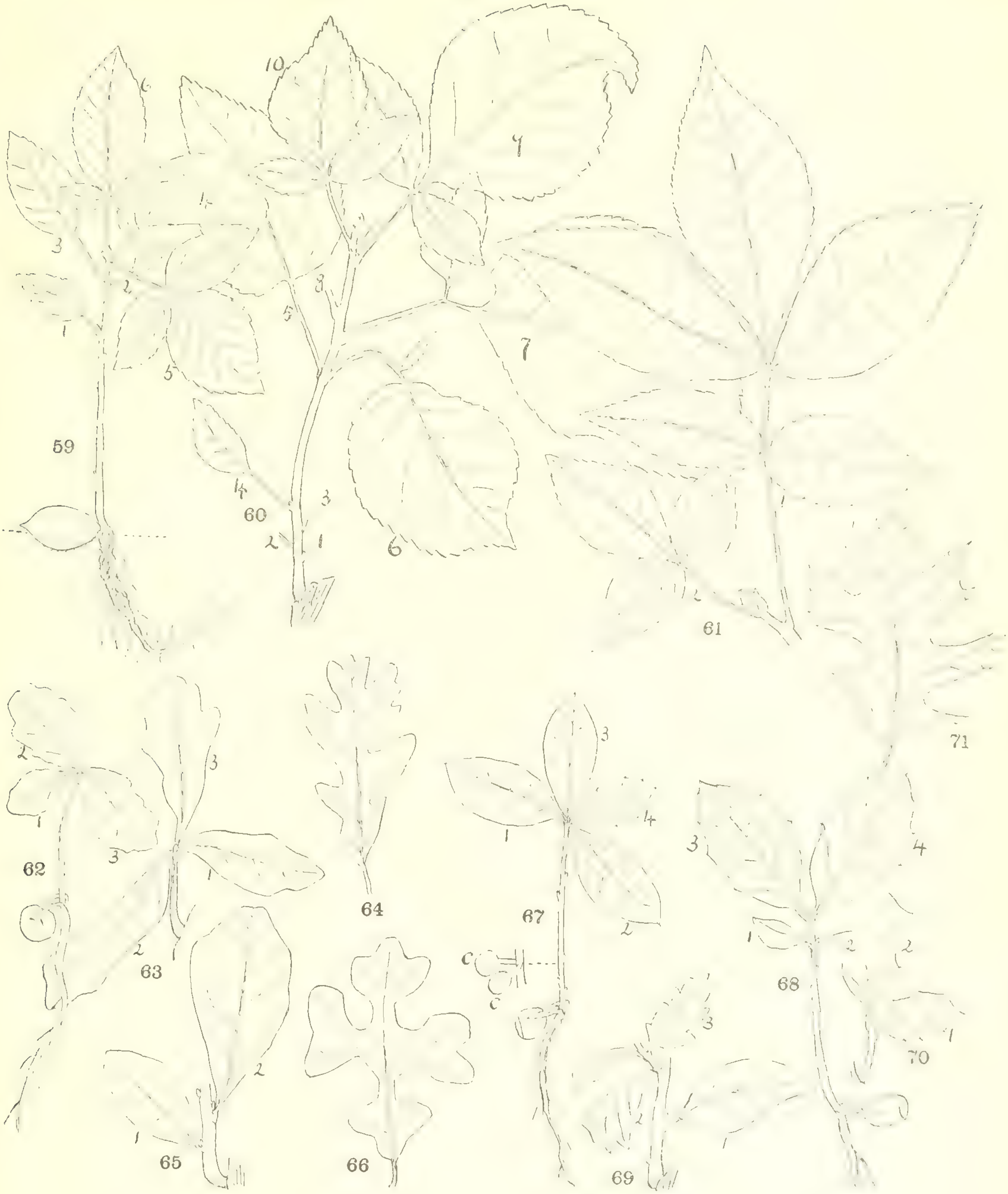


48

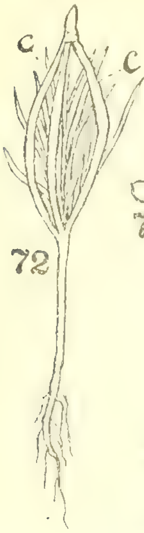
Jackson, Localized Stages.



JACKSON. LOCALIZED STAGES.

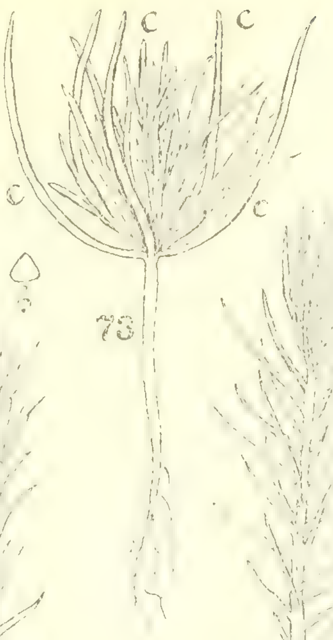


JACKSON, LOCALIZED STAGES.

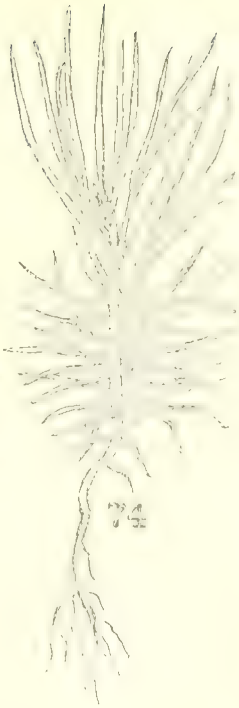


72

73a



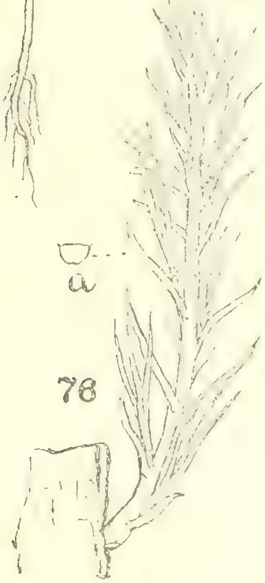
73



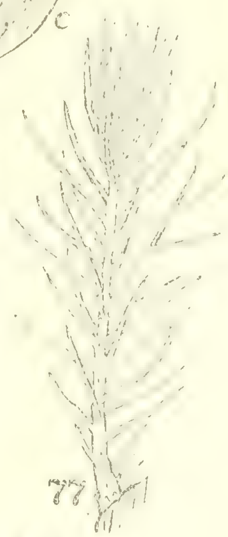
74

74

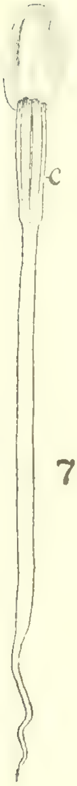
75



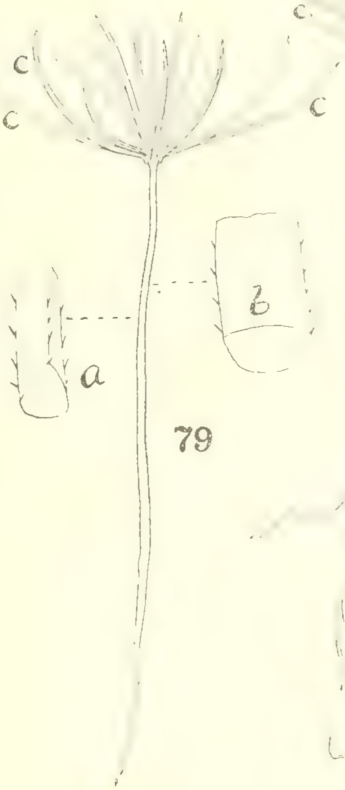
76



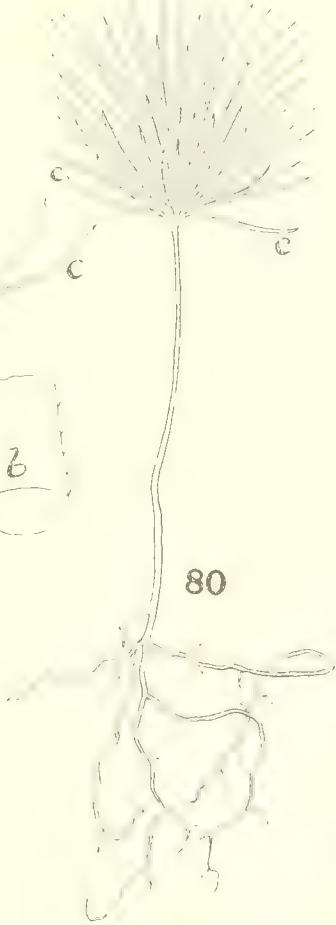
77



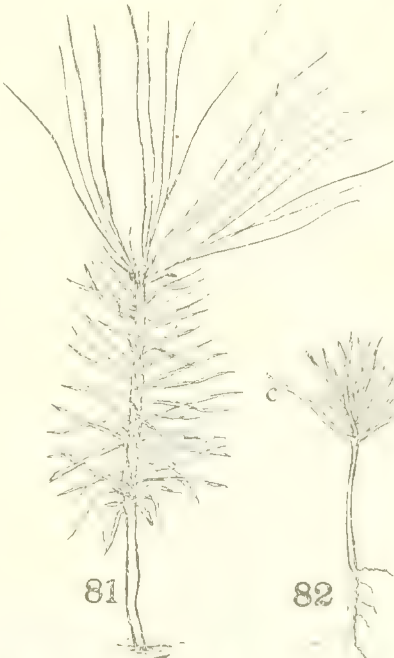
78



79

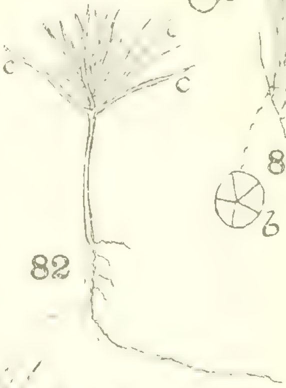


80

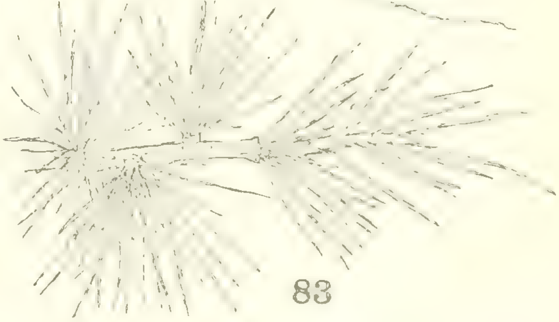


81

81a

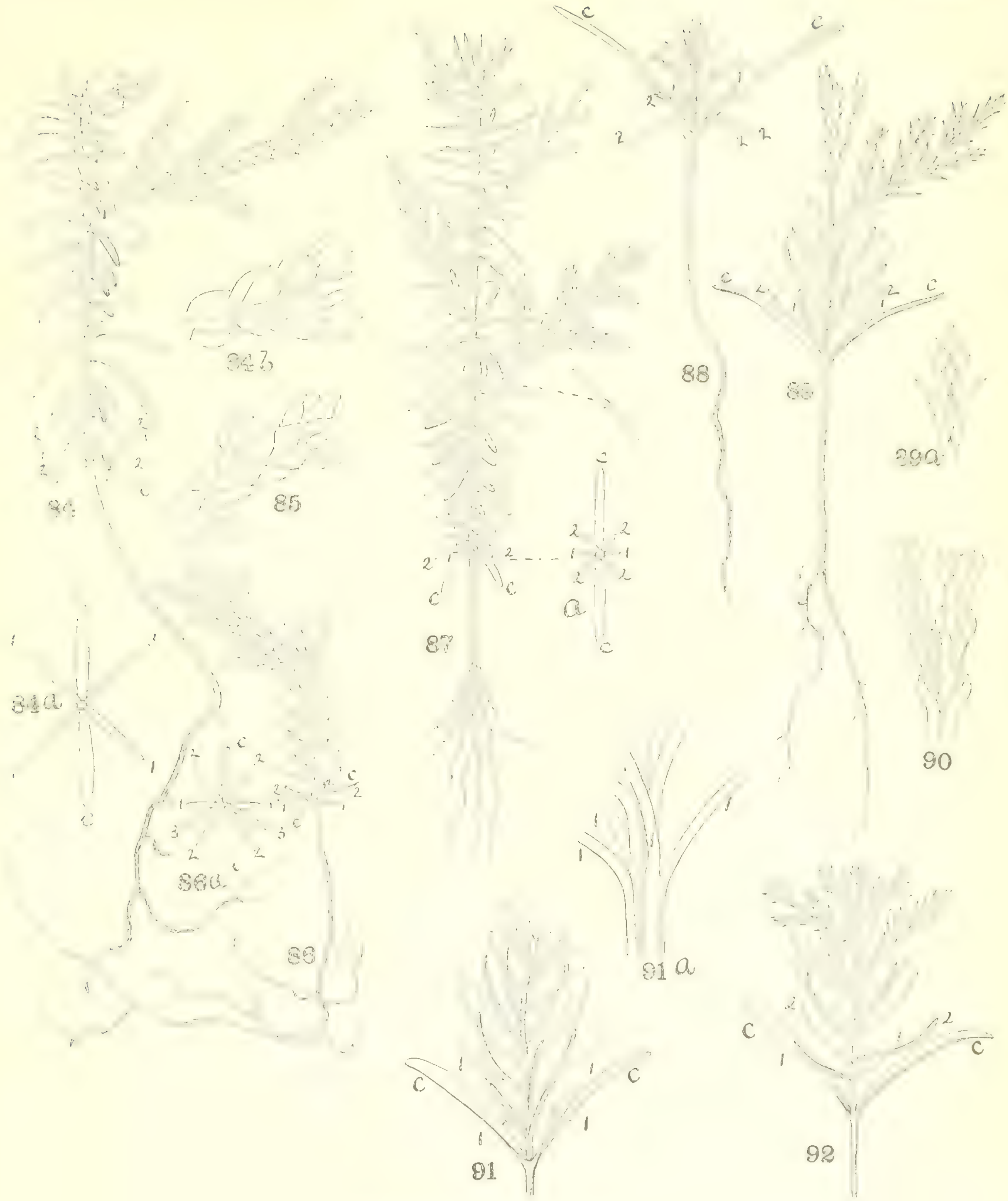


82

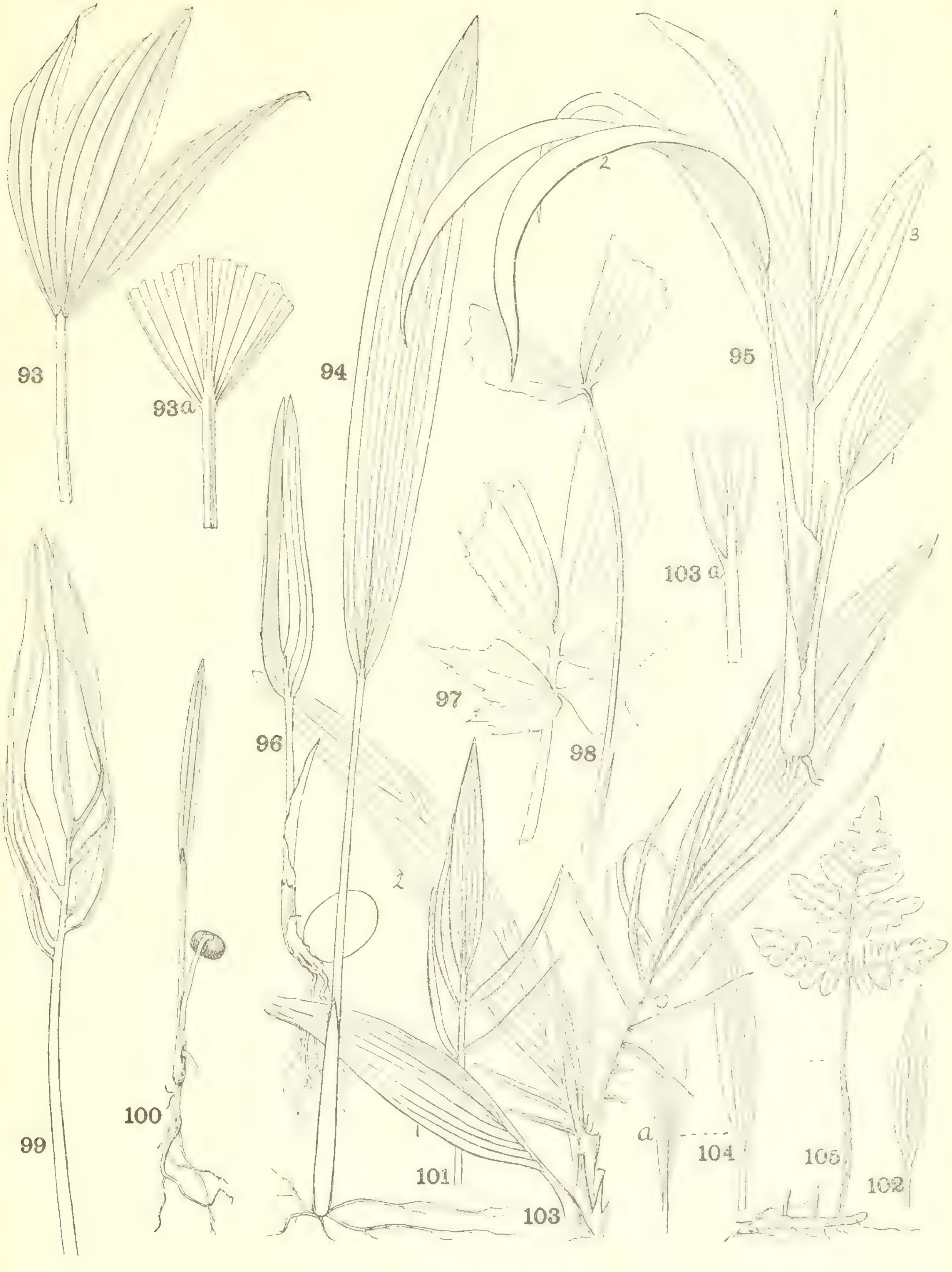


83

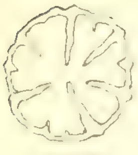
Jackson, Localized Stages.



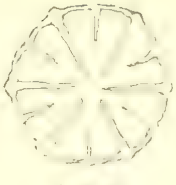
Jackson, Localized Stages.



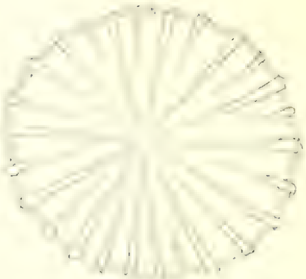
Jackson, Localized Stages.



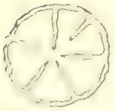
107



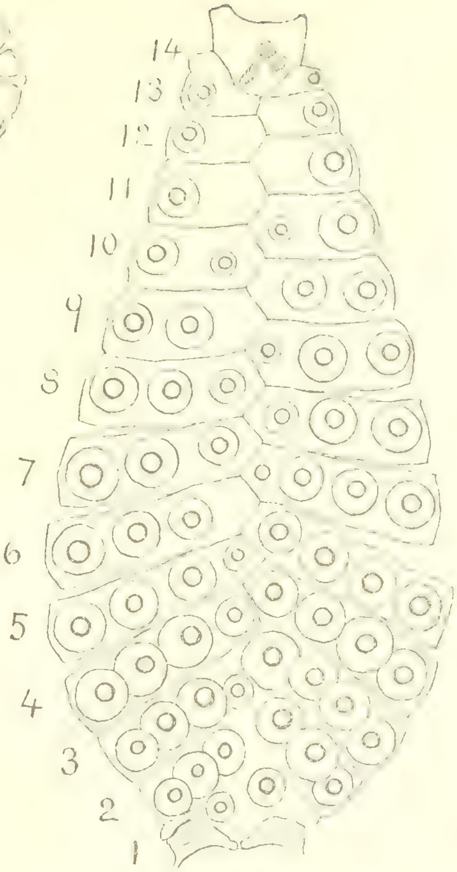
108



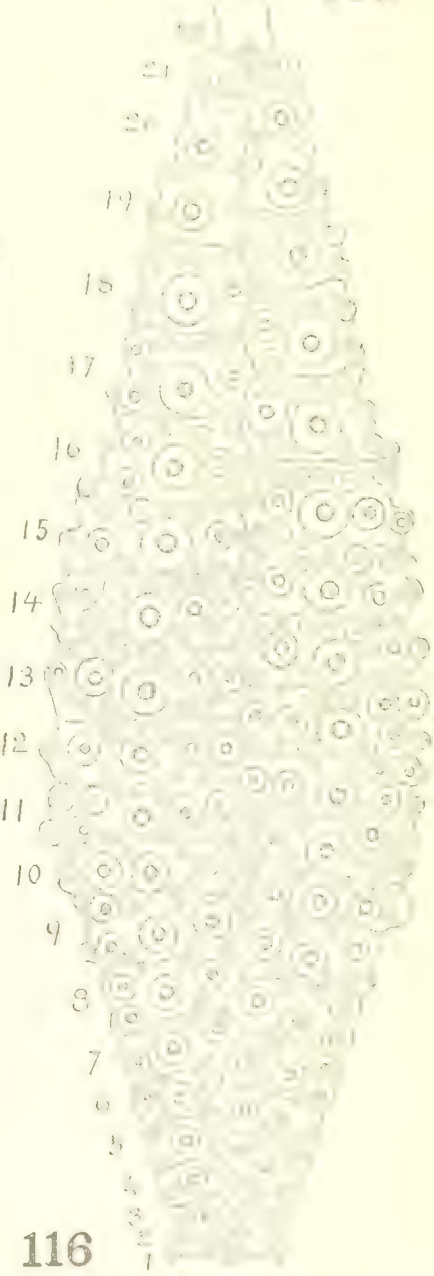
109



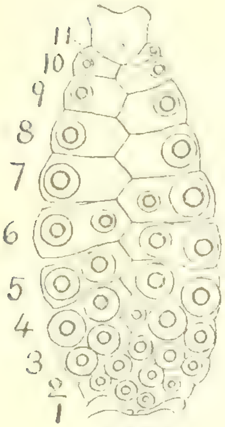
106



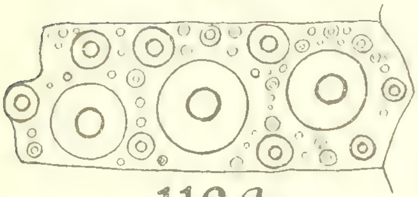
111



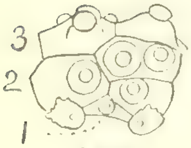
116



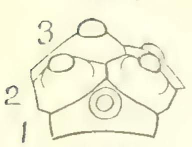
110



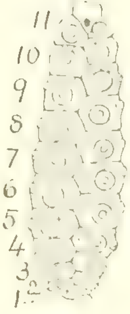
116 a



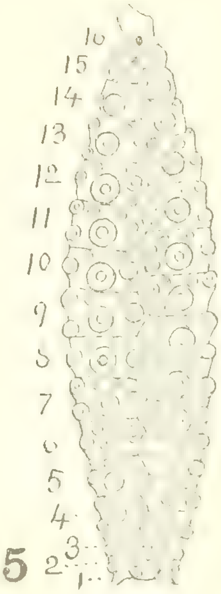
113



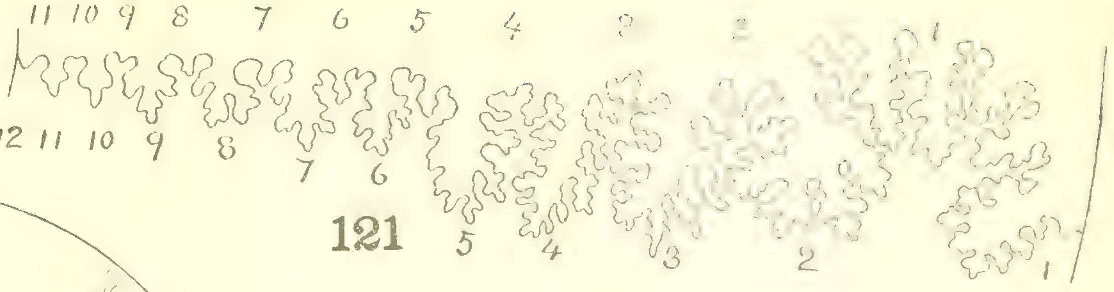
112



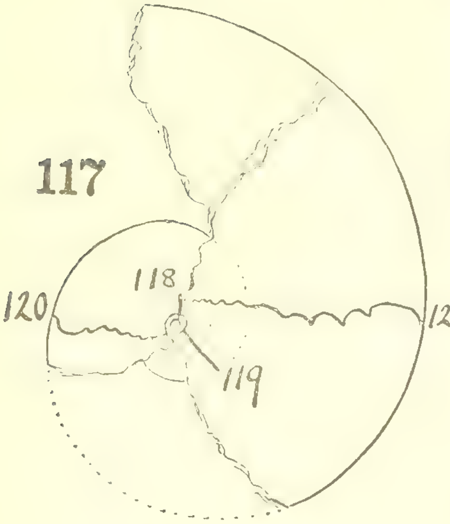
114



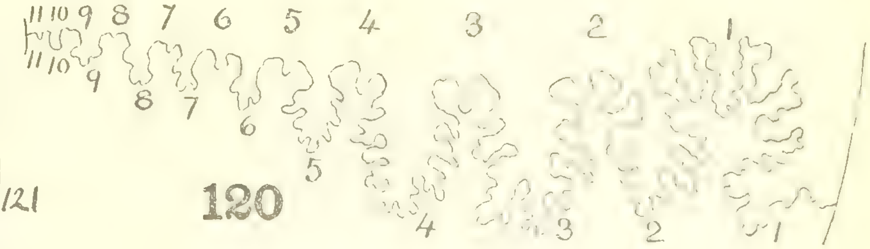
115



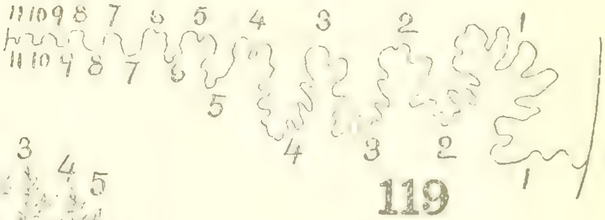
121



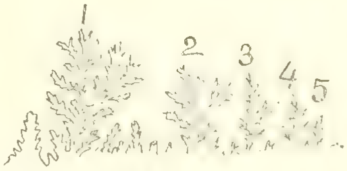
117



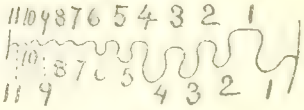
120



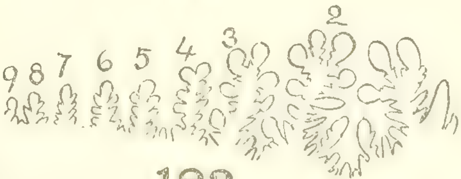
119



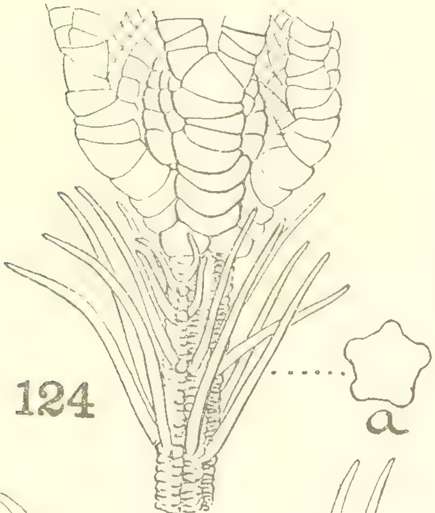
122



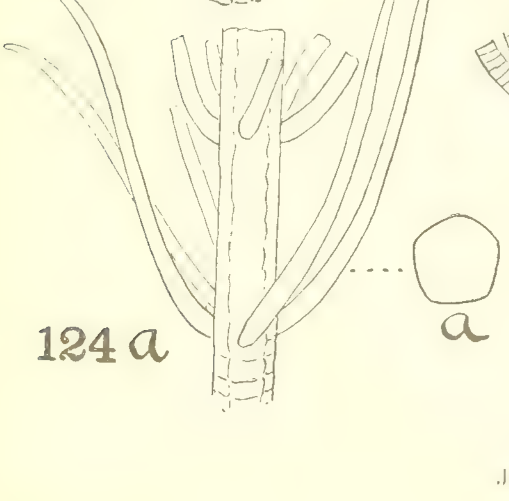
118



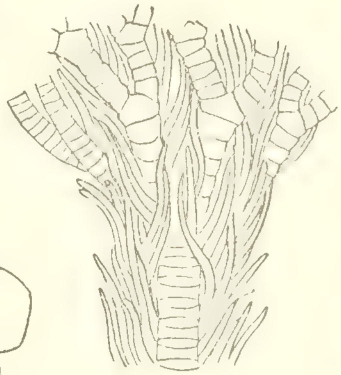
123



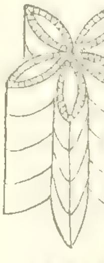
124



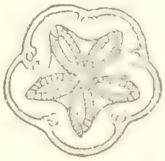
124 a



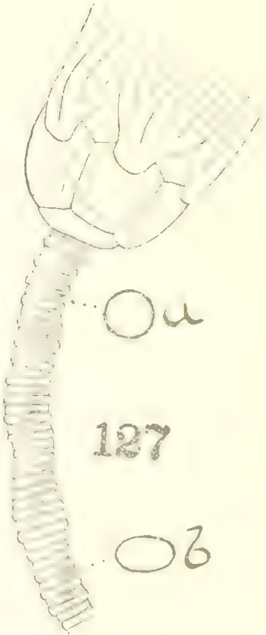
125



126



125 a



127

5. THE DEVELOPMENT, STRUCTURE, AND AFFINITIES OF THE GENUS EQUISETUM.

BY EDWARD C. JEFFREY.

(Read March 15, 1899.)

INTRODUCTORY.

DE BARY in his masterly Comparative Anatomy of the Vegetative Organs of Vascular Plants expressly renounces the consideration, of what he terms the *voir venir*, the course of development, and practically confines his attention to the structure of mature organs. It may be assumed, that this was done more to limit a task which he describes as a labor of the Danaids, than from any real distrust of the developmental methods, which yielded in his hands such splendid and lasting results in the study of Fungi. Since the appearance of De Bary's text-book there have been many researches on the development of the sporangia, spores, prothallia, archegonia, antheridia, embryos, and meristemata of vascular plants, and on the mature structure of their less accessible tropical representatives, and the still rarer fossilized remains of past ages; but in the midst of all this activity one developmental study has been almost entirely overlooked.

In his presidential address before the botanical section of the British association for the advancement of science, at the meeting of 1896, Dr. D. H. Scott (p. 2) makes the following remarks: — "The embryological method has so far received scant justice from botanists. * * * In the cases which have been investigated perhaps excessive attention has been given to the first division of the ovum, the importance of which, as Sachs showed long ago, has been overrated, while the later stages when the differentiation of organs and tissues is actually in progress have been comparatively neglected."

Convinced of the truth of this statement, the writer has devoted considerable attention to the study of the development of the young sporophyte, in all the various groups of vascular plants and his investigations have led to conclusions, which seem to have a not unimportant bearing on certain problems of the morphology and phylogeny of the phanerogams and vascular cryptogams.

The present memoir is devoted to the development and structure of the genus Equisetum alone; but in order that the questions presented by the ontogeny and anatomy of the Equisetaceae may be fully appreciated, it is necessary to indicate in a general way the relevant morphological conceptions which now prevail, and to state as briefly as possible.

the writer's position towards these conceptions, as the result of the studies mentioned above.

Further since the genus Equisetum may be considered in the light of the many and brilliant palaeobotanical researches of recent years, as the last degenerate survivor of a phylum, which begins in the petrifactions of the Silurian period, and extends with important modifications down to the present time, it will be necessary likewise to outline the structure of the various calamitean forms, with special reference to those features, which afford an adequate explanation of the peculiar anatomy of Equiseta, or which on the other hand can themselves only be understood by an accurate comprehension of the organization of the living representatives of the calimarian stock.

Morphology of the Central Cylinder.

Sachs (Lehrbuch der botanik, 1882, p. 74 *et seq.*) in the second edition of his Lehrbuch divided the tissues of the higher plants into three groups, the integumentary, fibrovascular, and fundamental. De Bary in his Comparative anatomy already referred to adopted the same morphological standpoint. In his conception the fibrovascular strands consist of Nägeli's xylem and phloem, and according as the xylem is completely surrounded by phloem, or by radially arranged clusters of phloem, or has the phloem applied only to one side, or to two opposite sides, he speaks of concentric, radial, collateral, and bicollateral bundles respectively.

In recent years Van Tieghem (Sur la polystélie, Ann. sci. nat. bot., sér. 7, tom. 3, p. 275; Traité de botanique, 1891, p. 673; Eléments de botanique, 1898, p. 83) has set up a very different hypothesis of the morphology of the fibrovascular system of the higher cryptogams and the phanerogams. The primitive type of vascular axis, according to his view, consists of a centrally placed stele (concentric fibrovascular bundle of De Bary), limited by a specialized inner layer of the cortex, the endodermis. This simple type of stele, which he calls monostelic, may be modified in various ways. It may for example divide by repeated dichotomy into two, four, eight, etc., exactly similar strands and thus become polystelic (Van Tieghem, Eléments de botanique, p. 179; Traité de botanique, p. 1370); or secondly, it may become enlarged and develop a central pith and radiating medullary rays, the parenchyma of which, is morphologically different from the fundamental tissues outside the stele. The fibrovascular strands which appear externally as the result of the formation of the medulla and its rays, are not morphologically comparable to the concentric steles of the polystelic type. This sort of central cylinder or stele, is found characteristically among the higher vascular plants, but occurs occasionally among the Pteridophyta, *e. g.* Osmunda and Todea; thirdly, in this type the endodermis may become infolded between the bundles and breaking in the bottom of the sinuosities, may unite round the individual collateral strands. The pith by this process is supposed to become continuous with the fundamental tissues of the outside cortex. This type of axis is denominated astelic and is said to be characteristic of the Equisetaceae, the Ophioglossaceae, and many limicolous phaenogamous orders *e. g.*, Ranunculaceae, Nymphaeaceae, Alismaceae, etc. This account by no means exhausts Van Tieghem's types, but is sufficient for the present purpose.

Strasburger (Histologische beiträge 3) in a recent comprehensive investigation of the anatomy of vascular plants, adopts Van Tieghem's views except in the case of the so-called astelic type, which he prefers to consider as monostelic, regarding the individual endodermal sheaths, which surround the bundles in this type, as not morphologically equivalent to the general endodermis, surrounding the complex of bundles in monostelic axes. This view is the result of two considerations; first, he is of the opinion that it is difficult to conceive that the pith of different species of the same genus should lie sometimes within and sometimes without the stele, as for example in the case of the Equisetaceae and Ranunculaceae; and, secondly, since he attributes a great physiological importance to the pith, in connection with the conductive functions of the central cylinder, he thinks it impossible to consider it as in any case separated from the bundles.

His first objection had really been anticipated by Van Tieghem (Journ. de bot., 1890, p. 365), however, in the case of the Equisetaceae. Van Tieghem there shows that the stem of the Equisetaceae is always astelic in the adult plant and that the pith is consequently always continuous with the cortex. Van Tieghem's theory however would scarcely allow of this explanation in the case of the Ranunculaceae, but it is not necessary to consider that group in the present connection. In the Equisetaceae, he has shown from Pfitzer's researches and his own, that the individual endodermal sheaths of the bundles and the internal general endodermis, where they occur, are at intervals continuous with the outer endodermis, and as Strasburger admits the morphological value of the outer endodermal layer, he must necessarily grant the same value to its inward extensions. In regard to his objection to separating the pith from the bundles very little need be said. The former is frequently absent or composed of dead cells, especially in perennial plants, so that in general it can scarcely have any very important conductive functions. Zenetti (Leitungssystem von *Osmunda regalis* Bot. zeit., 1895) has moreover recently shown that in *Osmunda regalis* where the presence of a distinct endodermis surrounding the leaf-bundles, makes it easy to decide, there are no strands of medullary tissue, accompanying the leaf-traces on their upward course, as Strasburger has suggested in connection with the important conductive functions, which he has assigned to the pith. We may accordingly conclude that Van Tieghem's conception of astely, in the case of the Equisetaceae at least, is not open to the objections suggested by Strasburger.

Van Tieghem's ideas, more or less modified by Strasburger's criticisms described above, have met with general acceptance and they are now found in almost all botanical text-books. As a consequence the morphological conceptions of Sachs and De Bary have been almost universally abandoned.

It is necessary to examine, whether these new ideas are really more in accordance with the facts, than those of Sachs and De Bary, and that this may be done more definitely the following citation from Van Tieghem's (Traité de botanique, 1891, p. 765) writings is put before the reader. "Le cylindre central étroit et sans moelle de la région inférieure de la tige, au lieu de se dilater, comme dans le cas ordinaire, au lieu de se rompre en faisceaux libéroligneux distincts, comme dans la structure astélique, s'élargit quelquefois en un ruban, qui bientôt se divise en deux par un étranglement médian. Chaque moitié s'aplâtit plus haut à son tour et se divise en deux et ainsi de suite." This is his description of the mode of development of his polystelic type.

In his essay on polystely (Van Tieghem, Ann. sci. nat., Bot., sér. 7, tom. 3) we do not find any specific instances, of the development of cryptogams, illustrative of the polystelic type. In a later publication, however (Traité de botanique, 1891, p. 1372), he gives the following brief account of the development of the stem of *Pteris aquilina*. "La Ptéride aquiline, par example n'a d'abord, jusque vers sa septième feuille, q'une stèle axile, plus haut, cette stèle se divise en une stèle dorsale et une stèle ventrale, formant un cercle unique ; c'est plus tard seulement que ces stèles produisent des branches qui séjournent dans l'écorce et y constituent un second cercle en dehors du premier." As this is the only example so far as I am aware, of a description on his part of the development of a cryptogamous stem of his polystelic type and as *Pteris aquilina* presents the greatest complexity of bundle-arrangement found among our common ferns, the writer proposes to describe briefly his own investigation of this form. The account here given does not depend on the study of isolated sections, but on that of numerous complete series of sections of the young stem, from the region of the foot to that where the characteristic arrangement of the bundles of the adult is reached.

Above the exit of the first leaf-trace the young vascular axis is a bundle-tube, which at first is so narrow, that no fundamental tissue is enclosed by it. Consequently in passing inwards we meet, first the external phloem, then the ring of vessels and innermost a core of phloem. At the height of origin of the fourth or fifth leaf, a core of fundamental tissue makes its appearance inside the internal phloem. Immediately above the point of origin of each leaf-trace there occurs a break in the continuity of the fibrovascular tube, which may be called the foliar lacuna. In the younger region of the stem, the internal and external bast-elements communicate through these lacunae, but, when the stem has reached the stage described above, where there is present internally a core of fundamental tissue, the latter communicates periodically also with the fundamental tissue outside the tubular axis. The writer has not been able to discover here any indication of the repeated dichotomous division which Van Tieghem describes as characteristic of the stele of the young polystelic axis. On the contrary, if his observations are correct, there is present from the very first, a hollow tubular fibrovascular axis.

After from nine to twelve leaves have been formed in this way, the young stem, which up to the present has grown perpendicularly upwards, bifurcates and the two equal divisions plunge into the soil, and henceforth pursue the horizontal course, which is characteristic of the adult rhizome. In consequence of this horizontal course, the leaves no longer originate in a spiral manner, as in the younger upright axis, but come off alternately from the sides of the young rhizome. As a result, the foliar lacunae occur on opposite sides of the fibrovascular tube and frequently overlap, so that in certain planes of cross-section, there is presented the appearance of independent dorsal and ventral steles.

In the meantime a rod of brown sclerenchyma, oval in transverse section, has made its appearance in the midst of the fundamental tissue occupying the center of the stelar tube. At a point about two or three centimeters from the region of bifurcation of the young rhizome, the dorsal wall of the stelar tube becomes involuted, and gives off a bundle into its cavity, which is quickly surrounded by a tubular sclerenchymatous sheath, formed by the bending round it from below, of the rod of brown sclerenchymatous tissue already mentioned. The ensheathed single central vascular strand gives off branches to the leaves and is from time to time reinforced by additions from above. Subsequently it divides dorsiventrally into two, in a manner which need not be described here, and the original vascular tube having in the meantime become transformed into a complex tubular network of strands, the state of affairs which is characteristic of the adult is reached.

As the result of the observations described in the foregoing paragraphs, the writer has reached the conclusion that the outer bundles are not cortical, as is stated by Van Tieghem, and that the two large inner ones, which he appears to have confused with the dorsal and ventral primary strands of the younger horizontal rhizome, are in reality medullary strands. That the outer series is primitive is indicated, moreover, by the fact that both the root-traces and the leaf-traces are attached to it.

The above account gives little support to Van Tieghem's theory of polystely, since the young vascular axis is first and always a tube and does not become successively divided into two, four, eight, etc., strands, as he describes. It might be supposed that the state of affairs in *Pteris aquilina* is possibly abnormal, but the writer is in the position to assert, from the examination of the development of a large number of vascular cryptogams, belonging to the most different groups, that the course of development in *Pteris aquilina* is quite typical, and that there is no evidence in any case which has come under his notice of the repeated dichotomy of the primitive strand which has been indicated by Van Tieghem. The writer's results in the example described moreover agree with those of Leclerc du Sablon (Ann. sci. nat. bot., sér. 7, tom. 11) for his figures and descriptions of the *younger* stages of the stem of *Pteris aquilina* are quite in harmony with the statements above. He has made the curious mistake, however, of regarding the mature rhizome of this species, as derived from an adventitious bud on the young plant, although Hofmeister's (Higher cryptogams, Ray soc., p. 213) account is correct in this respect.

The writer's study of the development of the stem in a wide range of North American and exotic Pteridophyta has led to the result that, in the vascular axes of stems, there are just two primitive types of stelar structure, *viz.*, the single concentric strand, and the tubular concentric strand, and moreover that all the varied complexities of the mature stem may readily be derived from these by the study of development in the individual cases.

There can be little doubt that the simple concentric strand is the more primitive type, and that the tubular concentric strand was subsequently derived from it. The writer is inclined to attribute the origin of the tubular type to the action of mechanical causes, but it would be out of place to discuss this subject at the present time. The two primitive types of stele described above may, however, be appropriately designated, protostelic and siphonostelic respectively.

In the protostelic axes of the Hymenophyllaceae we generally find the concentric type of stele, but in the genus Hemiphlebium (Prantl, Die Hymenophyllaceen, Plate 4, figs. 61, 62) the bast disappears on the lower side of the stele, which thus becomes collateral. The Ophioglossaceae afford examples of this unilateral degeneration of the bast in siphonostelic stems. From a study of the development of the young stem of species of Ophioglossum and Botrychium the writer is able to state that there occurs here the same stelar tube as in the young stem of *Pteris aquilina.* The two types differ only in the absence of internal bast in the former. The researches of Poirault (Recherches anat. sur les crypt. vasculaires, Ann. sci. nat., bot., sér., 7, tom. 8), and Van Tieghem (Journ. de bot., 1890) have demonstrated the presence of an internal endodermis in the young stem of various Ophioglossaceae. It is interesting also to note that the leaf-traces of *Botrychium virginianum* are concentric, and like those of the cycads retain in all probability a primitive type of organization, which has disappeared in the bundles of the stem.

Our examples have up to the present been drawn from the Filicales. The primary vascular axes of living Lycopodiales rarely present the phenomena of siphonostely. A good example, however, is to be found in *Selaginella laevigata* Blk., var. *lyallii* Spr. The stelar tube in this case resembles that of *Pteris aquilina* and has likewise a pair of medullary strands. In a photograph 1 (Pl. 27, fig. 1), the stelar tube appears with a lacuna in its side, where the vascular strand of a branch has been given off, this gap is the ramular lacuna. The leaves originate from the stelar tube, however. without causing any break in its continuity. Photograph 2 (Pl. 27, fig. 2) shows the restoration of the integrity of the tube below the point of origin of a subsequent branch.

In photograph 3 (Pl. 27. fig. 3), we have a copy of Williamson's figure (Phil. trans. roy. soc., 1881, Pl. 52, fig. 9) of the tubular stele of *Lepidodendron harcourtii.* The vascular tissues in this form are likewise arranged in a tubular fashion. The leaf-traces are small and cause, according to his description, no interruptions in the walls of the tube. Where a branch is given off on the contrary, as in the figure, there occurs a ramular lacuna. Both Renault (Cours de bot. foss., tom. 2, p. 71) and Gibson (Annals of bot., vol. 8, p. 192) have been struck by this resemblance between *Selaginella laevigata* var. *lyallii* and *Lepidodendron harcourtii* (other species of Lepidodendraceae had similar peculiarities, *e. g.*, Halonia, Ulodendron, and species of Sigillaria, etc.), and Bertrand (*Phylloglossum drummondii*, Arch. bot. Nord France, 1885, p. 71) considers his Centradesmideae (in part) as belonging to the same type.

In comparing these instances with the examples taken from the Filicales, it is to be observed, that while both cases represent siphonostely, there is this marked difference between them: in the filicineous stems the siphonostely is characterized by the occurrence of foliar lacunae, while in the lycopodineous axes it is related to ramular lacunae. Without going further into the matter at the present time, the hypothesis is presented that siphonostely has a mechanical significance, and that in the case of the Filicales, the siphonostelic modification of the vaso-skeletal tissues arose in connection with the support of large leaves. Among the Lycopodiales it made its appearance on the contrary, in relation to the support of secondary axes. We may consequently call the siphonostely of the Filicales phyllosiphonic, and that of the Lycopodiales cladosiphonic.

At this stage we come naturally to the discussion of the bearing of these morphological conceptions, assuming that they are well founded, on the phylogenetic position of the Equisetaceae. In this connection it is necessary to examine with some care both the structure and development of the genus Equisetum, and since certain of its features can only be understood in the light of a knowledge of its ancestors, it will likewise be necessary to refer as briefly as may be to the organization of the Calamites and Sphenophyllales. It will conduce to clearness and brevity of exposition to begin with the extinct groups and subsequently to describe their living representatives.

CALAMITES.

The Calamites first make their appearance in the Silurian deposits (Stur, Sitzungsberichte akad. d. wissensch. Wien, bd. 83, p. 409) but their petrified relics and casts are so rare in these earlier strata, that the upper Devonian and lower Carboniferous beds give us the first definite idea concerning the organization of the more primitive representatives of the group. One of the oldest Calamites of which we possess any detailed information is the genus Archaeocalamites Stur. (Stur, Abh. d. k. k. geol. reichsanstalt, Wien, bd. 8. Heft 1. Culm-flora d. mährischen-schlesischen dachschiefers. Heft 2 Culm-flora d. ostrauer u. waldenburger schichten.) In this form there is present the jointed stem which is characteristic of the modern Equiseta. The ridges and channels of the stem, however, differed from those of Equisetum in not alternating at the nodes. The leaves which originated in the nodal region and were not united into sheaths, but were quite free from one another and dichotomously divided. The roots also appeared in relation to the nodes and were often forked like the leaves. Branches were frequently present in the nodal region, but they do not seem to have been very numerous. Of the nature of the strobili of this genus, very little is known, as they have been very imperfectly preserved. The vascular frame-work, with which we are fairly well acquainted, as the result of the investigations of Göppert, Renault, and Solms-Laubach, had the same general features as that of Equisetum, differing only in its continuous strands, and its secondary growth in thickness by means of a typical cambium.

The Calamites proper, differed from Archaeocalamites in their generally undivided leaves, and the continually more pronounced (in more recent strata) alternation of their vascular strands at the nodes. They possessed, like the older type, a cylinder of secondary wood. Their strobili are comparatively well known and vary greatly in structural details, presenting throughout a marked contrast to Equiseta, in the probable division of their sporophylls into dorsal sterile, and ventral generally peltate sporangia-bearing segments (Scott, Cheirostrobus, Phil. trans. roy. soc., 1897, B). According to Williamson and Scott (Phil. trans. roy. soc., 1894, B. p. 864, 868, 890) their branches originated, in contrast to those of Equisetum, above the nodes. From Weiss (Steinkohlen-Calamarien, Heft 2, p. 34), we learn that the roots of the Calamites were attached either at the nodes or slightly to one side (he does not say, however, which side).

Most frequently calamitean remains occur as casts of the medullary cavities. These casts represent accurately the inner configuration of the fibrovascular cylinder and are consequently constricted at points corresponding to the nodal woody rings and channelled along the course of the primitive bundles. As the primary rays between the primitive bundles were bridged over more or less rapidly by the secondary wood, they appear merely as broad, rounded, longitudinal elevations on the cast between the depressions above mentioned. At one side of the nodal circular depressions and on the ends of the rounded ridges corresponding to the primary medullary rays, there occur frequently knob-like projections. Sometimes less marked tubercles appear in a similar position on the other side of the node.

Brongniart (Hist. des végétaux fossiles) who did not realize that he was dealing with casts, explained the larger nodules as representing rudimentary branches and roots (p. 109), and curiously enough considered them to occur on the upper side of the node, although he was clearly aware that in *Equisetum fluviatile*, which he used as the basis of his comparison, the roots and branches come off below the articulations, and alternately with the leaves (p. 103). The other and often absent zone of tubercles he explained as undeveloped leaves (Brongniart, *op. cit.*). His ideas concerning the rudimentary character of the organs represented by the tubercles probably originated from the observation that in specimens, which are otherwise apparently well preserved, the nodules in question are frequently entirely absent. Subsequent investigations, which need not be detailed here, established the fact that in branching rhizomes, the orientation of which can be inferred, the more conspicuous nodules of the cast occur below the node and at the upper end of the longitudinal ridges.

It has not been so easy to settle the nature of the anatomical features of the calamitean woody cylinder, which gave rise to the ring of more prominent tubercles. In photograph 4 (Pl. 27, fig. 4), which is copied from Williamson (Phil. trans. roy. soc., 1871, pl. 26, fig. 22), we see a tangential section of the primary bundles of a Calamite, which is so close to the medulla that the carinal canals of the protoxylem of the bundles are laid open. It is to be noticed, that the course of the bundles is the same as in Equisetum, except, that on the left of the figure no alternation takes place at the node. Above the node are represented the vascular strands belonging to branches, or as has been stated more recently (Williamson and Scott, Phil. trans. roy. soc., 1894, B., p. 876) to leaves.

It is to be observed that these writers assume for the Calamites a different relation of the branches to the nodes, from that obtaining in Equisetum, *i. e.*, that they originated above the node and not from the node, as in the latter (Williamson and Scott, *op. cit.*, p. 890). In the medullary rays, below the nodal wood, the parenchyma is seen in spots *l* to be somewhat disintegrated. In photograph 5 (Pl. 27, fig. 5) which is a copy of a figure (Williamson, Phil. trans. roy. soc., 1878, plate 20, fig. 23) representing a more external longitudinal section passing through the secondary wood, may be seen the branch-traces *m* (or leaf-traces as they were later called) no longer running free in the upper medullary rays, but arched over more or less by strands of secondary wood. In the lower rays disintegration has gone so far that actual cavities, *l*, have made their appearance. Such cavities were considered to be definite canals by Williamson (*op. cit.*, 1871, 1878), and he accordingly called them infranodal canals. He expressed the opinion that the larger series of tubercles described above, as occurring on the pith-casts of Calamites are moulds of these canals in stone. Subsequently in collaboration with Scott (Phil. trans. roy. soc., 1894, B., plate 78, fig. 11) he published a figure, which is reproduced in our photograph 6 (Pl. 27, fig. 6), which may be considered as representing a tangential plane of section, somewhere between those of the two former figures, reproduced in our photographs 4 and 5 (Pl. 27, fig. 4, 5). In this figure the traces making their exit in the superior medullary rays, are no longer considered as belonging to branches, but on the contrary to leaves (Phil. trans. roy. soc., 1894, B., p. 876).

Stur (*op. cit.*) from the study of the casts of various Calamites and of the stem of their modern representatives, the Equiseta has reached certain conclusions which it will not be profitable to consider fully. He states, however, that Williamson's figure, reproduced in our photograph 4 (Pl. 27, fig. 4), is inverted, and that the areas of disintegrated parenchyma, which by the inversion of the figure in question, he places in the upper medullary rays are due to the disappearance of leaf-traces. He enforces this contention by objecting that Williamson's figures make the branches arise above the node and not below it, as he thinks should be the case, from the analogy of Equisetum. He comes to the conclusion that the infranodal canals of Williamson are consequently supranodal indications of leaf-traces, and that the large nodules of calamitean casts, already referred to, are as a result above the node, which hardly follows from his course of argument. It is, moreover, in many cases certain that the larger nodules are below the nodal constrictions of the casts, for reasons which have been already indicated.

Weiss (Steinkohlen-Calamarien, Heft 2) has more recently discussed the vexed question of the tubercles, and after calling attention to Stur's inversion of the casts, expresses his opinion that the disputed nodules, probably represent the points of attachment of either roots or leaves. He realizes that their occurrence below the nodes, and in alternation with the vascular strands, makes it difficult to regard them as related to the leaves. This would seem to lead to the alternative, that they are the indications of the attachments of roots. He does not draw this inference, however, although he records the fact that the nodules are absent entirely, or very imperfectly represented, on parts of Calamites which are undoubtedly aerial (*op. cit.*, p. 24). He leaves the question of their interpretation open, having previously stated that he does not regard the nodules as casts of Williamson's infranodal canals.

Solms-Laubach (Fossil botany, Eng. ed., p. 301–315) discusses at length the organization of the calamitean stem, and the nature of calamitean casts. As a result of the consideration of all the evidence, he comes to the conclusion, that the more conspicuous series of nodules on the medullary casts of the Calamites are really infranodal, and agrees with Williamson in regarding them, as the result of the regular disappearance of tissues in the lower medullary rays, but considers that the disintegration is due rather to unequal maceration, than to the presence of any special organs or canals. The opinion of Graf zu Solms in such matters rightly carried great weight, and after its expression practically in favor of Williamson's view, the latter thought it no longer necessary to defend his hypothesis (Williamson and Scott, Phil. trans. roy. soc., 1894, B., p. 888).

Seward in his recent admirable treatise on fossil plants (1898, p. 324) adopts Williamson's explanation as quite proved, and does not even discuss the other views.

Renault (Etudes des gîtes minéraux de la France, fasc. 4, atlas) has recently published figures of tangential sections through the inner part of the secondary wood of Calamites, in which are represented the usual more or less constantly alternating vascular strands. Above the nodal anastomoses, and at the bottom of the upper medullary rays, are indicated radiating traces, *o*, which are stated in the description of the plates to be "aquiferous organs." Below them are represented smaller traces, *f*, embedded in the vascular strands, which are regarded by this author as leaf-traces. His "aquiferous organs" are undoubtedly the homologues of the "leaf-traces" of our photograph 6 (Pl. 27, fig. 6) copied from the monograph of Williamson and Scott. In the full descriptive text, which appeared three years after his plates Renault (Etudes des gîtes minéraux de la France, fasc. 4, p. 93) informs us that his figures, one of which is copied in our photograph 1 (Pl. 28, fig. 1) should be inverted, and that his "aquiferous organs" are really "organes rhizifères" which he regards as the equivalents of Williamson's infranodal canals. He states also that he has found roots in connection with the organs in question. These observations open up again the whole subject of the infranodal canals, and it is to be regretted that Renault has not given us reasons for the subsequent inversion of his figures.

As will be shown in the sequel, a consideration of the structure of Equisetum gives us criteria for explaining all the foregoing conflicting accounts and apparently for settling this much-disputed question.

SPHENOPHYLLALES.

There remains to be said something concerning the organization and structure of the Sphenophyllales. Like the Calamites and Equisetaceae, they had a regularly jointed and furrowed stem. The ridges of the stem did not alternate. The leaves somewhat resembled those of Archaeocalamites in being dichotomously divided, and were arranged in superposed whorls. The branches, according to the account of Renault (*op. cit.*,

p. 170), originated at the nodes, and he tells us that they came off from the stem between the leaves, and consequently like those of Calamites and Equisetaceae were not axillary.

The fructifications of the Sphenophyllales were cones of superposed verticils of sporophylls. These consisted of a dorsal sterile segment, and one or more ventral sporangiferous segments, bearing as a rule on their upper surface a single sporangium which hung inwards towards the axis of the cone. Solms-Laubach (Jahrbuch geol. reichsanstalt, 1895, vol. 45, p. 239) has recently described an interesting strobilus, *Bowmanites römeri*, belonging to this group, in which the sporangiophores are transversally peltate like those of the cycad Encephalartos.

The most interesting cone of this class, however, is that of which Scott (Cheirostrobus, Phil. trans. roy. soc., 1897, B.) has still more recently given an account. The sporophylls of Cheirostrobus are arranged in superposed verticils of twelve members. Each sporophyll consists of a dorsal and a ventral tripartite segment. The former is sterile, and the latter has each of its three divisions developed into a typical peltate sporangiophore bearing four sporangia. This author calls attention to the marked resemblance of his cone to the calamitean Palaeostachya and Calamostachys.

The internal features of structure in the stem of the Sphenophyllales were remarkable. There was a protostelic triarch, hexarch, or dodecarch (Cheirostrobus) central cylinder. The groups of protoxylem were generally distinguished by the presence of carinal lacunae as in Equisetum. The central cylinder was further characterized by the presence of a peculiar secondary wood. Other points of anatomy need not be considered here.

Observations on the Genus Equisetum.

The development of the prothallus of Equisetum has been very elaborately studied by Buchtien (Entwick. prothall. von Equisetum), and the writer's investigations accord in their results with his, so far as they have gone. The gametophyte consists of a median vertically growing fleshy axis terminated by meristematic tissue, in which it is not possible to make out a definite apical cell. From this terminal, actively dividing tissue lateral lobes are produced, to which the sexual organs have a definite relation. The main axis seldom forks in *E. limosum* and *E. arvense*, but frequently does so in the large prothalli of *E. hiemale* chiefly studied by the writer, and there may be as many as four or five secondary axes in the latter species.

The antheridia are formed at the tips of the lobes in a manner which has been often described and need not be referred to here. The antherozoids likewise do not require special description, as they have been fully investigated in recent years by Buchtien and Belajeff.

The archegonia, however, require more attention. They originate, as has been observed by other writers, frequently, but not invariably, near the base of a prothallial lobe. A superficial cell becomes more rich in protoplasm than its neighbors, and undergoes transverse division into nearly equal parts, in this respect presenting a contrast to the mother-cell of the archegonium of the isosporous Filicales, where the first division results in the formation of a shallow outer cell and a much deeper inner one, Pl. 26, fig. 1. The young archegonium in the two-celled stage resembles closely that of *Lycopodium clavatum* (Bruchmann, Ü. d. prothal. u. d. keimpflanzen mehrer. europ. Lycopod., Pl. 3, fig. 12; I am indebted to Dr. G. L. Goodale for calling my attention to this recent work) of the same age. Treub (Annales du jardin bot. de Buitenzorg, tom. 4, 5) unfortunately does not figure such early phases in the case of *L. cernuum* and *L. phlegmaria.* In Pl. 26, fig. 2, is represented a later stage, in which the inner cell has become equally divided by a second transverse wall. The outer cell at nearly the same time becomes bisected by a perpendicular wall. Frequently the outer cell at this time is still undivided, and in such cases the perpendicular row resembles the three cells of the young archegonium of the isosporous Filicales, but the significance of the cells in the two cases is very different, in the former they are cervical cell, cervical canal-cell and central cell; in the latter, cervical cell, central cell, and basal cell. It was probably an archegonium at this stage of development somewhat obliquely cut and consequently showing only part of the central cell, which led Campbell (Delt. of mosses and ferns, p. 430, fig. 223b) to make the statement that a basal cell sometimes occurs in the Equisetaceae.

Janczewski (Bot. zeit., 1872, p. 420), Sadebeck (Schenck, Handbuch d. bot., bd. 1, p. 196), and Buchtien (*op. cit.*, p. 25), all agree in stating that there is no basal cell in the archegonium of the genus Equisetum, and with this assertion my own observations on a large number of examples of *E. hiemale*, *E. limosum*, and *E. arvense* are quite in accord. Pl. 26, fig. 3, represents a young archegonium of *E. hiemale*, in which the central cell has already given off the ventral canal-cell, and as a result has become the egg-cell. The neck has become further developed and the cervical canal-cell is beginning to push its way upwards. In Pl. 26, fig. 4 is represented a nearly ripe archegonium. The neck remains short in *E. hiemale*. The cervical canal-cell has become longitudinally divided into two, a peculiarity which has only been described elsewhere in *Lycopodium phlegmaria* (Treub, Ann. du jardin bot. Buitenzorg, tom. 5, pl. 21, figs. 9 and 10). The ventral canal-cell has already begun to degenerate. Around the egg-cell cells are cut off from the prothallial cells, by walls parallel to its surface, a feature first observed by Hofmeister and confirmed frequently by subsequent writers. The development of the archegonium in *E. limosum* and *E. arvense* is practically identical with that of *E. hiemale*, which has been described above, and they have the same peculiar longitudinally divided cervical canal-cell. Pl. 26, fig. 5 represents a nearly ripe archegonium of *E. arvense.* In the two last mentioned species the neck is very much longer than in *E. hiemale* and consists of three or four tiers of cells. The uniform occurrence of longitudinal division in the cervical canal-cell of these three species is interesting and probably indicates that this feature will be found to be common to the group. Campbell (Mosses and ferns, p. 427), however, figures a transverse division for *E. telmateia.* Sadebeck (Engler u. Prantl, Nat. pflanzenfam., teil 1, abteil 4, p. 2) has recently published a figure of the archegonium of *E. arvense* which does not at all agree with Fig. 5, but as he does not represent in it the divisions of the prothallial cells parallel to the surface of the egg, and the cuneate insertion of the neck of the archegonium which have been noticed by practically all other observers, beginning with Hofmeister, his representation must be regarded as somewhat diagrammatic.

The first division of the egg is transverse, the basal wall being generally somewhat oblique. The inclination of the basal septum is sometimes towards the apex and sometimes towards the base of the prothallus, more frequently, however, towards the former. It has not been possible to absolutely settle the order of the next two divisions, but it is probable that the median wall is formed first. The transverse wall often does not extend at first entirely across the embryo, especially in the hypobasal half. The apical cell is early formed in the epibasal portion, and in the hypobasal half, an apparent apical cell is also differentiated. These features are shown in Pl. 26, fig. 6, which is almost identical with Hofmeister's (*op. cit.*, Pl. 39, fig. 2) illustration of a similar stage. The development of an apparent apical cell in the lower half of the embryo, and a tacit homologizing of that region with the corresponding region, as regards the substratum of the leptosporangiate embryos, with which he was familiar, led him into the error of regarding it as the embryonic primary axis. As its regular segmentations soon cease, and it is thrust aside by the growth of the upper portion of the embryo, he regarded the primary axis of Equisetum as abortive. The real primary stem-apex in the upper part of the embryo of Pl. 1, fig. 6, he regarded as that of a secondary shoot, an error which has been recognized by Sadebeck (Pringsheim's Jahrbücher, bd. 11, p. 581), and subsequent observers. Sadebeck (*op. cit.*) informs us that in the case of *E. arvense* and *E. palustre*, the development of which he has studied, the epibasal cell gives rise immediately to the primitive shoot-axis, from which the first whorl of leaves is derived exactly as are the subsequent ones. This statement I am not able to confirm exactly, for in *E. hiemale*, which I have particularly studied, the rudiment of the first root appears very early, next the apical cell, and on the side of it which faces the apex of the prothallus. Pl. 26, fig. 7, shows an embryo at this stage, the cells of which have been outlined with the camera lucida. *a* is the apical cell and *r* is the rudiment of the root. It might be thought that another cell, further down on the right of the young embryo, is really the radical rudiment, but that such is not the case may be determined from the next figure, which is a drawing of an older embryo made with the camera lucida. The upwardly directed arrows in the two last mentioned figures indicate the direction of the neck of the archegonium, and those pointing downwards, the position of the embryos in relation to the substratum, as inferred from the course of the prothallial root-hairs. It will be seen from these figures, that the root appears very early in *E. hiemale*, and in all probability is derived from the epibasal region of the embryo. It presents in the latter feature a close correspondence to the state of affairs observed by Treub (*op. cit.*) and Bruchmann (*op. cit.*) in the embryos of *Lycopodium cernuum*, *L. phlegmaria*, *L. clavatum*, and *L. complanatum*. The segmentations of the apical cell become numerous before the first whorl of leaves makes its appearance in embryos of nearly twice the size of that of Fig. 8. It is accordingly not easy to trace the members of the first foliar whorl to the epibasal octants by allowing, as is usually done, one for the apical cell, and one for each of the three primary leaves. It would seem to be a more reasonable procedure to compare the embryo of Equisetum rather with those of the Lycopodiales, concerning which we have in recent years so much information, which was entirely lacking when the fashion of comparing all embryos with those of the probably highly specialized leptosporangiate ferns originated. Such a comparison would lead to our deriving both root and shoot from the epibasal half of the embryo, and leaving the whole hypobasal portion for the foot. Without, however, attaching too much importance to this comparison, it may be safely stated that the primitive root of *E. hiemale* originates high up on the side of the embryo and in close relation to the primitive shoot. As the embryo develops, the root gradually descends, and finally as it begins to push its way out, becomes the most inferior organ of the embryo. The young root is directed towards the apex of the gametophyte and alternates with the two anterior leaves of the first foliar whorl. The first so-called adventitious bud originates above the point of origin of the first root, and likewise between the two primary leaf-traces. The secondary axis differs from the primary in not producing the rudiment of the root, till the first foliar whorl is clearly indicated, as a fold round the secondary stem-apex. About the time of the appearance of the first adventitious bud, and when three or more whorls of leaves have been formed on the young axis, the shoot breaks through the calyptra, the root having previously in the case of *E. hiemale* and *E. arvense* made its way into the soil. In *E. limosum* the root develops very slowly and does not enter the soil till long after the shoot has made its way out. This is probably the result of its amphibious mode of life, as many plants of this habit have a poorly developed primary root e. g., *Nelumbium luteum*. The writer has not a sufficiently complete series of embryos of *E. arvense* and *E. limosum* to describe completely the embryogeny of these species. Moreover, the examination of the earlier phases of development is rather to be passed over in this essay since a good deal of attention will be given to the later stages which have been almost entirely neglected by previous writers.

The first shoot of *E. hiemale*, after bursting through the calyptra, forms from six to twelve segments, and then ceases to grow. Some time previously, however, the first so-called adventitious shoot has emerged below the point of attachment of the first foliar whorl of the primary axis. This secondary axis is terminated inferiorly by a root which originates below its primary whorl of leaves or ochreola. The secondary axis is followed by a tertiary axis which springs from below its first sheath and between two leaf-traces. These features are represented in Pl. 26, figs. 9, 10. The next figure shows us a somewhat older plant, in which a number of shoots have been successively formed in the order indicated by their numeration. It is to be observed that each shoot has a corresponding root. In the stouter later shoots the nodal buds, which develop normally as shoots, are no longer confined to the basal nodes, but appear also in relation to the higher articulations, as may be learned from Pl. 26, figs. 10, 11. As each new axis originates well down towards the attachment of the root of its predecessor, the later formed shoots are continually more deeply buried in the soil, Fig. 11. In *E. hiemale* twelve or more erect shoots are formed before a horizontal rhizome makes its appearance, from the base of one of the larger and more deeply buried secondary upright axes. It would be interesting to discover if the depth of the parent axis in the soil has anything to do with the formation of these plagiotropic shoots; the writer, however, has not made any experiments in this direction. The first shoot of *E. hiemale* has foliar sheaths of three members, the second shoot has frequently similar sheaths, but more often has whorls of four united leaves, then follow axes with verticils of four, five, and six members.

The writer's cultures of *E. limosum* did not produce plants of more than two developed shoots. It is apparently difficult to secure the proper conditions for the continued growth of this species, for, unlike *E. hiemale*, it does not live long under greenhouse conditions. Here the first shoot may have leaf-whorls of only two members; in fact, the plants grown from spores obtained from a swamp about fifty miles northeast of Toronto, were practically all characterized by this peculiarity. Buchtien (*op. cit.*, p. 40) has noticed a similar peculiarity in the case of *E. variegatum*. Sporophytes from spores gathered by the writer from plants on the border of Howard Lake in High Park, Toronto, had, on the other hand, almost invariably sheaths of three members. A study of the sporogeny showed that in the former case a considerable number of spore-mothers became disintegrated after the tetrad division had taken place. This did not occur in the material from High Park. It is possible that, in the first instance, too large an amount of sporogenous tissue had given rise to spore-mothers and too little to the formation of tapetal cells, and, as a consequence, the resultant spores produced only depauperate plants. A series of observations in this direction might prove interesting in connection with Bower's theory of the origin of the sporophyte. Pl. 26, figs. 12 and 13, sufficiently illustrate the external features of the young sporophytes of *E. limosum*, and show that they do not differ essentially from those of *E. hiemale*, except in their greater delicacy, and in the smaller number of segments formed in the first shoot.

Turning our attention now to the internal development of *E. hiemale*, we find that in the first axis of the young sporophyte there is a gradual transition from the typical arrangement of the tissues in the root, to that obtaining in the base of the young stem. The central cylinder of the first shoot makes its appearance as an unbroken tube of reticulated tracheides. There are no typical protoxylem elements, although the internal tracheides are formed first. The primitive vascular axis, in fact, starts out with a similar organization to that which is found subsequently to recur at the nodes. The center of the vascular tube is occupied by parenchyma, which may be considered in the light of what is to follow, as belonging to the pericycle. Outside the ring of reticulated vessels occurs a zone of phloem, terminated by a typical endodermis, with the usual radial lignified bands. The rudiment of the second shoot causes an interruption in the continuity of the vascular cylinder of the primary axis above its point of origin which disappears again, at about the level of exit of the leaf-traces from the central cylinder. The latter do not cause any gaps in the vascular ring as they pass off, and it is only at a measurable distance above their points of origin, that the so-called foliar lacunae make their appearance. The first shoot-bud originates between two leaf-traces as do all the subsequent ones. The foliar lacunae described above, if they may so be called, divide the fibrovascular tube into three distinct strands which alternate with the leaves. These three strands differ from the woody ring below in having typical protoxylem elements, which lie in more or less characteristic carinal lacunae. They are surrounded by a common external endodermis. At a point two or three millimeters above the exit of the leaf-traces of the primary whorl, a cell makes its appearance in the midst of the internodal bundles, which is characterized by having endodermal markings on its walls; still higher up this gives place to a radiating group of cells, which have endodermal dots about the middle of their radial walls. Just above the exit of the leaf-traces of the next whorl, that is at the base of the next internode, the internal endodermal elements disappear. They again become evident at a short distance above this point, only to disappear again above the exit of the leaf-traces of the next internode. These variations recur in all the segments of the first shoot and need not be further described. In the higher internodes, however, the internal endodermis shows a tendency to unite with the outer one, just below the continuous rings of reticulate vascular tissue which mark the nodes. It is impossible, however, even in the unbroken series of thin sections, which the writer has studied, with the aid of phloroglucin and hydrochloric acid, to be sure that such a union actually takes place, as the indications consist only of somewhat irregular endodermal streaks radiating out from the internal endodermis, at the points described above. From the state of affairs in the adult stem (Pfitzer, Pringsheim's Jahrbücher, bd. 6; Van Tieghem, Journal de botanique, 1890, p. 365 *et seq*), it might be expected that we should find similar indications just above the nodes, but they do not occur.

The first node of the second shoot has likewise a pith of pericyclic origin. Here again the internal endodermis makes its appearance only above the primary node. The internal endodermis of the second shoot, however, is continuous throughout the secondary axis and does not disappear at the nodes. It clearly unites moreover with the outer endodermis below the nodal vascular rings. In subsequent shoots the internal endodermis is likewise continuous and finally in shoots of five or more bundles it is found also in the primary node and is continuous with the internal endodermis of the parent axis. It is in shoots of five bundles that the internal endodermis first unites with the external, above as well as below the nodes, as in the adult plant. The primary axis does not develop nodal buds other than the basal one, except in some of its higher nodes, and these seldom under ordinary conditions give rise to branches. The second, third, and subsequent shoots have one or more dormant nodal buds at all their nodes. Quite frequently there is an increase in the number of vascular strands in passing from a lower internode to a higher one. In one example, where four strands were present in the first internode, five were found in the second and six in the third, after which the number remained constant. This feature is interesting, as repeating on a small scale a phenomenon which was of common occurrence among the Calamites.

Equisetum limosum is very similar to *E. hiemale* in the particulars of its internal development. The only differences which need to be noticed are those which have reference to the distribution of the endodermis. In the first shoot of this species, whether bifascicular or trifascicular, there are no indications whatever of an internal endodermis, although as may be seen from photograph 2 (Pl. 28, fig. 2) the outer endodermal sheath is well developed. The second shoot of *E. limosum* in my specimens was too immature to show the endodermal marking.

The arrangement of the endodermis in the young stems of these two species of Equisetum does not appear to offer very much support to Van Tieghem's (Journ. de botanique, 1890, p. 370) hypothesis of astely, for in accordance with his conception of the origin of astely, the primitive type had above the first whorl of leaves, bundles individually surrounded by endodermal zones, and these individual zones becoming subsequently fused gave rise to a continuous outer and a continuous inner endodermis. It is not unreasonable to expect to find some evidence of this in the young stem. If anything may be argued from these embryological results, the primitive condition would seem to have been one in which there was both an outer and an inner endodermis. This subject, however, will be more satisfactorily discussed at a subsequent stage.

Having examined the external and internal development of the young sporophyte of Equiseta we may now turn our attention to certain features of the adult, which are either in themselves interesting, or which are of importance in coming to any conclusions concerning the affinities of the Equisetaceae.

Photograph 3 (Pl. 28, fig. 3) represents a transverse section through the nodal region of the subterranean stem of *E. hiemale.* On the outside of the stem and on the carinal ridges are to be seen certain projecting organs, *a*, of a parenchymatous nature. These are situated opposite the points where the leaf-traces leave the central cylinder to pursue their upward course in the foliar sheaths. They were noticed by Brongniart (*op. cit.*) in *E. litorale*, but apparently have not been elucidated since. At *b* in the same photograph may be seen the origin of a root-trace. At *c* there is present a shoot-bud. This has several roots attached to its lower end which do not appear in the plane of section. Photograph 4 (Pl. 28, fig. 4) represents more highly magnified one of the organs referred to above. The sclerenchymatous cortex of the rhizome is here interrupted by a strand of parenchymatous tissue which extends from the leaf-trace outwards. These organs may be conveniently called nodal organs. Their constituent parenchymatous tissue is of a loose and spongy nature, and their organization is quite similar to that of the lenticels which occur on the roots of the higher plants, and we probably shall not go very far astray in considering that these peculiar nodal organs of certain Equiseta have the function of permitting an interchange of gases through the otherwise impervious integument of the rhizome. They make their appearance on the subterranean parts of quite young plants of *E. hiemale* as well as in the adult.

Photograph 5 (Pl. 28, fig. 5) shows an entire thin transverse section through the nodal region of *E. silvaticum.* At *a* are the nodal organs similar to those of *E. hiemale.* The origin of root-hairs from the epidermis of the rhizome may also be clearly made out. The outer zone of the cortex is parenchymatous, and internal to it occurs a ring of brown sclerenchyma, the continuity of which is broken by the spongy parenchyma of the nodal organs or by root-traces, *b*. Inside the sclerenchymatous zone occurs a third, which is of a parenchymatous nature and adjoins the bast of the fibrovascular bundles. The central cylinder is seen to give off six processes, five of which are root-bases and one a dormant branch, *c*. Alternating with these and much smaller are the leaf-traces, *d*, subtending internally the nodal organs, *a*, where these are present. The central cylinder in the nodal region, as has been often described, forms a continuous ring in which the vascular tissue, instead of being scanty and separated into individual bundles, each characterized by an internal lacunar protoxylem, as is the case in the internodes, is massive and entirely devoid of typical protoxylem elements. At the lower side of the photograph the leaf-traces have quite cleared the central cylinder, and it is to be noticed as a feature of importance, which will be subsequently referred to more at length, that the nodal vascular ring is quite unbroken by their exit. In the upper part of the figure, the medulla is seen to extend outwards into the root-bases.

Photograph 6 (Pl. 28. fig 6) is of a section through the nodal region of *E. arvense.* The nodal organs are absent in this species, but the rhizophoric buds, *c*, are better developed than in *E. hiemale* and *E. silvaticum.* The fact that the so-called foliar lacunae do not appear immediately above the leaf-traces, as they should from the analogy of the Filicales, but are separated from them by the nodal wood, may also be inferred from this section, which on the whole closely resembles that of *E. silvaticum.* Nodal organs have been found by the writer only in *E. hiemale* and *E. silvaticum*, and are absent in *E. variegatum*, *E. arvense*, and *E. limosum.*

In the next photograph (Pl. 29, fig. 1) is shown part of the section through the node of *E. limosum.* In this species all the nodal buds develop as rhizophoric organs except one or two. At *c* is the single large ramular bud and at *b* are the rhizophoric organs. The other features of the section need not be described.

Turning our attention now to the longitudinal topography of the stem of Equisetum we have in photograph 2 (Pl. 29, fig. 2) a tangential section of the nodal region of *E. hiemale* the plane of which is sufficiently deep to lay open the vallecular canals, *l*, of the lower internode; a branch, *c*, is making its way out through one of these. The magnification is sufficient to show that the medulla of the branch is composed of brown sclerenchymatous cells, and that its wood, which is no doubt to be regarded as the nodal wood of the first segment of the branch, is devoid of lacunae, such as occur in the internodes, and forms a ring, the vessels of which are still immature on the upper side. Above the branch are present four leaf-traces, *t*, which are about to assume an upward course in the foliar sheath of the main stem. The more profound tangential section of photograph 3 (Pl. 29, fig. 3) shows clearly the arrangement of the fibrovascular bundles at the node. Each bundle from the lower internode widens out at the node and the contiguous strands become thus united. From this ring of nodal wood the bundles of the upper internode take their origin in alternation with those of the inferior internode. A branch, *c*, is starting from the lower border of the nodal wood between two lower vascular strands, and, although the plane of section is so deep as to pass through the very base of the branch, there is still a wide brim of nodal wood above the latter. The leaf-traces, as may be learned from the examination of a series of tangential sections, originate on a level with the lower surface of the branch-traces, but as they pass outwards, rapidly pass above the latter, as may be inferred from photograph 2 (Pl. 29, fig. 2).

A deep tangential section is likewise represented in photograph 4 (Pl. 29, fig. 4). The arrangement of the bundles at the sides is the same as in the preceding photograph, but the two central bundles, between which a cluster of thick-walled cells indicates the starting-point of the medulla of a branch, do not alternate but are continued with those of the internode above. This phenomenon is not rare in *E. hiemale* and is of interest both because it has apparently not been noticed before in Equiseta, and because it exemplifies a mode of fascicular arrangement which was common at the nodes of the Calamites.

Radial sections show more clearly than tangential ones the relations of the branches to the nodal wood, and it is the more necessary to devote some attention to these features, because the opinion prevails that the branches of the Calamites in contrast to those of Equiseta originated above the node. Photograph 5 (Pl. 29, fig. 5) shows the topography of a radial section of an aerial stem of *E. hiemale*, at the point of origin of a branch. At *d* is the partially sclerified nodal diaphragm of the main stem, and below it at *n* is the nodal wood. From the lower half of the nodal vascular ring comes off a branch, *c*. The diaphragm of the first node of the branch is very deep, and is somewhat sclerified at the ends. Two roots, *r*, and a nodal bud, *k*, are attached to the basal node of the branch. The first leaf-sheath, or ochreola, is present inferiorly, but is abortive on the upper axial side. It is manifest that the aerial branch of *E. hiemale* arises neither above nor below the node but from the lower region of the nodal wood. Photograph 6 (Pl. 29, fig. 6) illustrates the topography of the origin of a rhizophoric bud from a node of the rhizome. The same general features obtain as in the last photograph, and it may readily be seen that here, too, the potential secondary axis originates from the lower region of the nodal wood. The lettering is the same as in the preceding photograph. A feature which is worthy of note is that, the first sheath of the bud, the future ochreola, is normally developed, as is generally the case in branches derived from the subterranean stem. The next photograph 1 (Pl. 30, fig. 1) illustrates the mode of origin of a stout upright branch from a deep horizontal rhizome; as before, *d* is the diaphragm, *n* is the nodal wood, and *r* is a root. Here, too, the branch arises neither above nor below the node but from the nodal wood, and since in this case the base of the secondary axis is very broad, it covers the whole of the node.

The next photograph 2 (Pl. 30, fig. 2) is of a radial section through the nodal region of the rhizome of *E. silvaticum.* The branch, as in the other cases, originates from the lower region of the nodal wood.

From all these examples it will be sufficiently obvious that in Equisetum the branches arise neither above nor below the nodal wood but from it, and in the case of the smaller branches, from its lower border, and in that of the larger ones, more or less exactly from its central region. In *E. limosum* at the subterranean nodes, whether of upright or horizontal stems, there are present one or two branch-buds and a number of rhizophorous buds. From the latter as many as six or seven roots grow out into the soil, and the stem-region of the buds more or less completely degenerates. That these root-bearing pedicels are the morphological equivalents of branches is obvious for two reasons: in the first place they possess a typical medulla like the shoot-organs, and are thus distinguished from the pithless roots which are characteristic of the modern Equiseta; secondly, by examining the successive nodes of an upright branch, beginning below the soil and passing upwards, it is possible to distinguish all phases of transition between rhizophoric organs and typical leafy shoots These results are only confirmatory of those of Janczewski (Recherches sur le dév. des bourgeons dans les prêles. Mém. soc. nat. sci. Cherbourg, 1876, tom. 20), but it is important to have independent evidence in these matters as will appear in the sequel.

It has already been stated that the leaf-traces originate from the protoxylem of the bundles of the lower internode. Photograph 4 (Pl. 30, fig. 4) demonstrates the accuracy of this statement. The leaf-trace is separated rather widely from the surface of the nodal wood, and the endodermis forms a deep bay on the outer side of the node, between it and the leaf-trace, as is represented in Pl. 26, fig. 14.

Before leaving this part of the subject one interesting feature may be referred to. Photograph 5 (Pl. 30, fig. 5) represents a section of the nodal diaphragm of *E. hiemale.* It is easy to make out that the cells of the upper portion of the diaphragm are arranged in perpendicular rows, and that the lower members of the rows have become thick-walled, forming the characteristic sclerification of the diaphragm. These features are of considerable interest, because peridermal tissue has been recently described as occurring in the diaphragms of Calamites by Williamson and Scott (Phil. trans. roy. soc., 1894, B., p. 889). In the Calamites, however, there was no subsequent sclerification of its cells, the nodal diaphragms of this group being entirely parenchymatous (Williamson, Phil. trans. roy. soc., 1871, p. 505). A similar sclerified periderm has been found by the writer in *E. limosum.* In *E. silvaticum, E. arvense,* and *E. variegatum,* on the other hand no nodal periderm is present. The presence or absence of this feature may be of some use in the difficult task of tracing the relationships of the modern Equiseta. The palaeobotanical writers above referred to compare the periderm of calamitean diaphragms with that abnormally formed in the pith of certain Campanulaceae, etc. It is probably equally justifiable to compare it with that occurring in certain cryptogams. Russow (Vergleich. untersuch., p. 117), for example, has described the existence of periderm in the Marattiaceae and the Ophioglossaceae and the writer (Trans. Can. inst., 1898, p. 284) has called attention to a similar formation at the bases of fallen leaves in *Botrychium virginianum*. The frequent separation of the stem of equisetoid plants at the nodes, as the result of normal or exceptional conditions, would make such a protection at these points of considerable importance. In this connection it is interesting to notice that the sclerified diaphragms of *E. limosum* extend to the outer margin of the vallecular canals. They thus surround the vascular bundles, just as is the case with the abciss-periderm of the leaf-stalks of Hippocastanum, etc.

Some of the results described in the foregoing paragraphs seem to the writer not to be without importance in connection with certain disputed points of calamitean anatomy referred to in the Introduction. The two features which are most worthy of consideration in this connection are the mode of insertion of the branches of the Calamites, and the nature and position of the organs which gave rise to the inferior series of nodules on calamitean medullary casts.

The Branches and Infranodal Canals of Calamites.

Beginning with the first of these, the statement is commonly made by palaeobotanical writers that the branches of the Calamites in contrast to those of Equiseta originated above the node. Photograph 6 (Pl. 30, fig. 6) of the present memoir is a copy of a rare and beautiful specimen of a calamitean stem showing external features, figured in Weiss's admirable monograph (Steinkohlen-Calamarien, Heft 2, atlas, pl. 16, fig. 6). Several nodes are present, to which leaves are attached and the scars of a number of fallen branches are to be seen in a single horizontal row. On the lower margin of the branch-scars are smaller scars, which Weiss interprets as belonging to fallen leaves, but when he tells us that these fallen leaves are the appendages of a node which comes immediately below the branches, it is probable that the botanical reader, remembering the state of affairs in Equisetum, will hesitate to follow him. If a node is present in this position it is certainly not very obvious and is irregularly placed. Moreover, in similar specimens figured in an earlier monograph (Weiss, Steinkohlen-Calamarien, Heft 1, atlas, pl. 17, figs. 1 and 2), where the leaves were represented only by their scars, in accordance with the conviction that the branches arise above the node, he has considered the smaller scars, related to scars of fallen branches, as dipping down underneath the branches and coming up to the nodal line again in the intervals between the branches. In the example figured here, since the attached leaves are obviously situated in some cases immediately above the scars of the branches, he abandons that position, and assumes the presence of an intercalated node corresponding to the crescentic series of smaller scars on the lower margins of the branch-scars. The writer suggests that the crescentic rows of scars of the figure, copied in photograph 6 (Pl. 30, fig. 6), really belong to the basal whorls or ochreolae of the fallen branches and that as a consequence, so far as can be judged from external appearances, the branches of Calamites had the same relation to the node as those of Equiseta. The ochreolae of the Calamites were not continuous sheaths as in Equisetum but were composed of separate leaves. The ochreolae of the Equiseta not infrequently lack fibrovascular bundles and are often obsolete on the upper axial side of the branch. The occurrence of similar features in the Calamites is not improbable and these would account for the absence of leaf-scars on the upper margin of the branch-scars and for the non-retention of the ochreolar leaves, together with the normal leaves of the nodes of the parent axis in photograph 6 (Pl. 30, fig. 6).

But without attaching too much importance to the above explanation, it will be well to consider the internal relations of the branches to the nodes, as described in recent works on calamitean anatomy, and, at the same time, to examine the statements as to the nature and disposition of the organs which gave rise to the infranodal tubercles of certain calamitean casts.

In photograph 6 (Pl. 27, fig. 6), a copy, the original of which has been already indicated (Williamson and Scott, Phil. trans. roy. soc., 1894, B., pl. 78, fig. 11), is a representation of the nodal arrangement of the vascular strands of a Calamite, as seen in tangential section. It will be observed that these have, generally speaking, the same relation to each other at the node as is exemplified in our photograph 3 (Pl. 29, fig. 3) of *E. hiemale*. In the lower ends of the upper medullary rays are situated certain structures which Williamson and Scott (*op. cit.*, p. 876) consider to be leaf-traces. In photographs 4 and 5 (Pl. 27, figs. 4, 5), which are taken from Williamson's earlier memoirs (Phil. trans. roy. soc., 1871, pl. 26, fig. 22; ibid, 1878, pl. 20, fig. 23), these are represented as being the vascular strands of branches. The changed interpretation of the later memoir need not be considered for the present, although, as will be indicated subsequently, it is of some importance. In the later memoir already referred to, Williamson and Scott (Phil. trans. roy. soc., 1894, B., pl. 78, fig. 11) make the statement that the leaf-traces in the Calamites originated from the protoxylem of the bundles of the lower internode, and consequently, it may be assumed, below the nodal wood, since they inform us that the protoxylem came to an end below the node in Calamites, just as it does in the Equisetaceae. Returning now to the statement that the leaf-traces are found in the upper medullary rays and consequently above the nodal wood, it may be asked how they have got into this supranodal position. It can be only in one of two ways: they must pass up on either the inside or the outside of the nodal wood. But before considering either of these possibilities, one of their figures (*op. cit.*, pl. 78, fig. 7) shows the leaf-trace running directly outwards from the protoxylem of the lower vascular strand and consequently below the node. This is a difficulty in connection with either of the above suggestions. Let us suppose that it does not exist, however, and imagine the leaf-trace to pass upwards inside the nodal wood. But this would involve the presence of ringed and spiral woody elements on the inside of the nodal wood, since the leaf-trace consists largely of these elements. They state, however (*op. cit.*, p. 872 and 877), that protoxylem is absent from the inside of the nodal wood of the Calamites just as it is in Equisetum. These difficulties make us turn to the other alternative, that the leaf-traces pass to their supranodal position on the outside of the nodal wood. Photograph 4 (Pl. 27, fig. 4) is a reproduction of a figure from one of Williamson's memoirs (Phil. trans. roy. soc., 1871, pl. 26, fig. 22). The section which it represents is so profoundly tangential that the carinal canals of the protoxylem are laid open. The so-called leaf-traces are nevertheless already in their supranodal position, and consequently cannot have passed up external to the node. If, in spite of all these difficulties, the leaf-traces are still maintained to start outwards in the lower ends of the supranodal medullary rays, other difficulties make their appearance. All figures which indicate the internal relations of calamitean branches represent their vascular strands as running in the medullary rays and at the same time above the nodal wood. Since, according to Williamson's and Scott's statement (*op. cit.*, 1894, B., pl. 78, fig. 11), the leaf-traces also run in the same rays and in the same relation to the nodes, the branches must originate in the axils of the leaves, which is not only contrary to the arrangement in Equisetum, where the branches originate between the leaf-traces, but also to the statements of Williamson and Scott themselves (*op. cit.*, p. 864, 868, 890) that a similar state of affairs obtained in the Calamites. There is, in fact (Williamson, *op. cit.*, 1871, pl. 28, fig. 38), a figure of a branch in this anomalous position in one of Williamson's older memoirs, but the joint authors of the later memoir already referred to (*op. cit.*, 1894, B., p. 890) tell us that this represents an arrangement which was exceptional. It is not easy to see, however, why it should not have been present whenever the strands alternated at the node, as they inform us they generally did (*op. cit.*, p. 868, 876, 877), since in such cases the leaf-traces and the branch-traces would both run, according to their descriptions, in the superior medullary rays. If we return to Williamson's original statements (*op. cit.*, 1871 and 1878) that the strands running in the upper medullary rays belonged to branches, the difficulties are just as great; for here, too, since the strands of the lower internode generally alternated with those of the upper, the branch falling in the interval between the two upper strands would be exactly over a lower strand, but from the lower strand the leaf-trace originated and consequently the branch would lie in the axil of the leaf, which is not the case.

If the cause be sought of all the manifold contradictions, which, assuming the correctness of the writer's course of argument, are present in the figures and statements cited above, it is to be found in the fact, that the figures in question are inverted, in other words, in the fact, that, contrary to what is the case in Equisetum, the branches of the Calamites are represented as originating above the nodes, and by inverting the figures above mentioned all the difficulties which have been described at once disappear. It may be further stated, that it is only possible for the branches to uniformly alternate with the leaf-traces, whether the arrangement of the strands at the nodes is continuous or alternating, when the former originate between the strands which run up to the nodes, since it is from these same strands that the leaf-traces are derived both in Calamites and Equiseta.

But if the conclusions of the last paragraph be accepted as correct, Williamson's areas of macerated parenchyma no longer lie below the node, and consequently cannot be used as an explanation of the tubercles occurring below the nodal constrictions of calamitean medullary casts.

At this point the following quotation from Renault (*op. cit.*, p. 89) may be introduced apropos of photograph 1 (Pl. 28, fig. 1), copied from his monograph (*op. cit.*, atlas, pl. 47, fig. 7).

"Les lames de tissu fondamental qui séparent les coins ligneux s'élargissent à leur partie supérieure *o* planche 47 fig. 7, 8 (ces deux figures doivent être vues retournées) et forment une sorte de gouttière ou de canal allant de la moelle à la périphérie; en coupe transversale ces organes ont une section elliptique; il n'est pas rare de trouver une cavité dans la région centrale, produite par la disparition, de cellules polyédriques qui forment une sorte de moelle (M. Williamson les a désignés sous le nom de *infranodal canals*): les cellules qui composent la couche périphérique sont allongées dans le sens radial, prismatiques, polygonales sur une coupe transversale et rectangulaires sur une section faite suivant leur largeur, leurs parois portent des ornements ponctués; il est assez fréquent de voir des trachéides se detacher des coins ligneux, pénétrer au milieu de ce tissu particulier et se confondre avec lui, leur nombre est égal à celui des lames de tissu fondamental secondaire qui séparent les coins ligneux. Les racines adventives, quand elles se développaient, étaient en rapport avec ces organes, que nous considérons comme des organes particuliers expectants, que nous distinguerons sous le nom d'organes rhizifères."

The three important features of this citation are, that Renault states that his figure, which is reproduced in our photograph 1 (Pl. 28, fig. 1), should be inverted, that the traces running in the medullary rays are related to roots, and that they are equivalent to Williamson's infranodal canals. Renault gives no reasons for the inversion, but obviously the figure, in its original position, is open to the same objections as have been urged in a former paragraph against the orientation of the similar figures of Williamson and Scott. The observation that the organs, *o*, have a parenchymatous medulla which is surrounded by a zone of pitted cells comparable to the peculiar tracheary elements of the basal node of the branches, or of the walls of the rhizophorous pedicels of Equiseta is all the more interesting, because, as Renault informs us, roots are actually attached to these organs. It is possible to accept his first two statements, without admitting the accuracy of the third, *viz.*, that the organs, *o*, are the equivalents of Williamson's infranodal canals. If the reasoning of a former paragraph is sound, the tracts of macerated parenchyma which Williamson called infranodal canals are not really below the node at all but on the contrary above it, consequently the organs described by Renault cannot be considered as their equivalents. If Renault's figure, reproduced in photograph 1 (Pl. 28, fig. 1), be compared with photographs 5 and 6 (Pl. 27, figs. 5, 6), it is not very difficult to decide that the organs situated in the upper (really lower) medullary rays of the three figures are equivalent, and since, if the course of reasoning adopted here is correct, these organs in photographs 5 and 6 (Pl. 27, figs. 5, 6) are branches they must similarly be branches, or their homologues, in photograph 1 (Pl. 28, fig. 1). But Renault tells us, in the passage quoted above, that in this case they are related to roots, and the inference may be drawn, that they are the morphological equivalents of the rhizophoric buds of Equiseta, which have an identical relation to the vascular strands and to the nodes.

Renault (*op. cit.*, texte, p. 92, 95, 107, 123) has not realized this, since both in his figures and the subsequently published explanatory text he makes the traces of the ordinary branches pass outwards above the leaf-traces and above the node, and not below the leaf-traces and at the node, as must be the case if the mode of the argument previously adopted by the writer is not fallacious.

At the beginning of the discussion of the relation of calamitean branches to the node, a figure from Weiss, our photograph 6 (Pl. 30, fig. 6), was cited, indicating, if the writer has properly interpreted it, that externally at least the branches of the Calamites had the same relation to the node as obtains in living Equiseta. A consideration of the internal features has led, moreover, to a similar conclusion in regard to the position of the branches in the ancestors of the Equisetaceae. In the case of the calamitean rhizophoric organs on the other hand, first from the evidence of internal structural arrangements, the conclusion has been reached that they are the equivalents of branches and have the same relation to the nodes, Pl. 26, fig. 17, which is a copy from Weiss (Steinkohlen-Calamarien, Heft 1, p. 121) shows clearly that the roots and branches were on the same side of the node in the Calamites, externally as well. In the center of the figure to the left are seen a few small leaf-scars. Along the rest of the nodal line these have disappeared. Below the indications of leaf-traces stretches a line of scars, the smaller of which are root-scars the single larger one is a branch-scar, below which are the less distinct scars of its basal roots.

Assuming the correctness of the various arguments employed in attempting to solve these difficult questions of calamitean anatomy, the result is reached, that in the Calamites the branches and their morphological equivalents, the rhizophoric organs, had the same relation to the nodes as in living Equiseta. Further, the branches were more or less exactly centered on the node according as they were of greater or smaller size. The rhizophoric organs were attached along the lower margin of the ring of nodal wood, and their cylindrical medullary cavities, which, unlike those of normal branches, did not expand are consequently represented on the casts by nodules situated below the nodal constrictions. The infranodal tubercles are thus only to be found on subterranean stems, and this is in accordance with Weiss's statement (*op. cit.*, Heft 2, p. 24) referred to in the Introduction, that they are absent or inconspicuous on axes, which are clearly recognizable as aerial.

An attempt has been made in the foregoing paragraphs to explain certain features of the Calamites by reference to the corresponding features of living Equiseta. The writer will now employ the reverse method of attempting the explanation of certain structural features of the extant genus Equisetum by a consideration of the homologous ones of the ancestral and extinct Calamites.

The Cladosiphony of the Equisetaceae.

Attention has been called in the early part of this essay to the peculiar relations of the leaf-traces in Equisetum to the nodal wood *viz.*, that they originate below it and yet without causing any gap or lacuna in its vascular ring, as might be expected from the analogy of the foliar lacunae of the Filicales, which occur immediately above the exit of the leaf-traces from the vascular tube. Yet, notwithstanding the fact that the lacunae do not begin at the level of exit of the leaf-traces, they do, nevertheless, occur opposite the outgoing traces, but only make their appearance above the nodal wood. These facts have already been referred to in connection with photographs 5 and 6 (Pl. 28, figs. 5, 6). They appear not to have been noticed by previous writers and are susceptible, nevertheless, of a somewhat interesting interpretation which is of importance from the standpoint of the phylogeny of the Equisetaceae.

In the Introduction attention has been called to the characteristic arrangement of the traces at the nodes in Archaeocalamites, which is diagrammatically represented in Pl. 26, fig. 16. It is to be noticed here that the leaf-traces are not opposite lacunae at all, but, on the contrary, the branches or their equivalents, the rhizophoric organs, are. In this primitive type of Calamite the leaf-traces were not subtended by any gaps in the vascular tissues, but the internodal lacunae were ramular lacunae and appeared immediately above the branches. In the Introduction the term cladosiphonic has been used to describe a tubular fibrovascular axis characterized by having ramular lacunae but no foliar lacunae, and consequently Archaeocalamites, like *Selaginella laevigata* and *Lepidodendron harcourtii*, is cladosiphonic. But Stur (*op. cit.*, p. 158) has shown that in the Ostrau beds, passing from lower to higher strata, a series of forms, *Calamites ramifer* Stur, *C. cistiformis* Stur, *C. approximatiformis* Stur, and *C. ostraviensis* Stur, represent transitions from the bundle arrangement of Archaeocalamites represented in Pl. 1, fig. 15, to that of Equisetum represented in Pl. 1, fig. 16. It will consequently be not unreasonable to infer with Stur, that the equisetal arrangement of the bundles was derived in the course of geological time from archaeocalamital arrangement. The final result of the shifting of the internodes upon each other at the nodes has been, that the lacunae primarily belonging to the branches no longer subtend the latter but on the contrary the leaf-traces, which still, however, betray their true morphological relations by the fact that their exit causes no break in the nodal wood. It may then be assumed, if the reasoning based on these facts is correct, that the apparent foliar lacunae of Equiseta are really ramular lacunae which have shifted from their original position during the course of evolution of the Equisetales, and that this group is accordingly cladosiphonic. The original state of affairs occasionally reappears even in modern Equiseta, as is shown in photograph 4 (Pl. 29, fig. 4). A much more striking example of the same ancestral phenomenon is shown by photograph 3 (Pl. 30, fig. 3), which reproduces the course of the vascular strands in the cone of *Equisetum arvense.* It will be noticed that the bundles in this case for the most part do not alternate. This feature is more or less marked in the cones of all the species of Equisetum which have been examined by the writer. In this connection may be mentioned a striking cambium-like arrangement of the cells in the young bundles of the cones of *E. hiemale* and *E. limosum.* It disappears, however, almost entirely in the comparatively massive bundles of the adult cone, and perhaps may also be regarded as an ancestral feature, since secondary growth was frequently present in the vascular tissues of the strobili of various Calamites.

It has been pointed out in the Introduction that protostelic and siphonostelic axes may be possessed by different species of the same genus *e. g.*, *Lepidodendron selaginoides* was protostelic and *L. harcourtii* was siphonostelic, likewise *Sigillaria vascularis* and *S. pulcherrima* had protostelic axes, while on the other hand *S. diploxylon*, *S. elegans*, and *S. spinulosa* had siphonostelic axes; a similar relation exists between *Selaginella martensii* and *S. laevigata*. In other instances different genera of the same natural order may exemplify the two types of stelar structure *e. g.*, in the Gleicheniaceae, Gleichenia is protostelic and Platyzoma is siphonostelic. Similar examples are afforded by the Hymenophyllaceae and Schizeaceae.

THE ANCESTORS OF THE EQUISETACEAE.

In this connection the question may properly be asked where are the protostelic Equisetales to be found. The Sphenophyllales immediately suggest themselves in reply to this question. Stur (*op. cit.*, p. 17) and Rothpletz (Botanisches centralblatt, Gratis beilage 3, pl. 11), have both called attention to their remarkable external resemblance to Archaeocalamites in their strobloid fructifications, their rigid and articulated stems, and whorled superposed dichotomous leaves. The branches of the Sphenophyllales also resembled those of the Equisetales in rising at the nodes, *between* the leaves (Renault, *op. cit.*, texte, p. 170). Solms-Laubach (*op. cit.*) has described the sporangiophores of *Bowmanites römeri* as peltate and Scott (*op. cit.*, 1897, B.) has compared the much more complex sporophylls of Cheirostrobus with those of the calamitean Palaeostachya, and makes the important suggestion that the comparison of the cone of the Equisetales with that of Cheirostrobus is likely to change considerably our views of the morphology of the former. He probably has in mind the extension of the comparison to Calamostachys, Paracalamostachys, Cingularia, etc., where the sporangiophore does not immediately suggest itself as the ventral segment of the sporophyll, as it does in Palaeostachya. Even in the latter genus the sporangiophore more often as in the case of the sporangium of the living Selaginella (Goebel, Bot. zeit., 1881, p. 697; Bower, Phil. trans. roy. soc., 1894, B., p. 523), appears to originate from the axis than from the ventral surface of the dorsal sterile segments. Weiss (Steinkohlen–Calamarien, Heft 2, p. 7) has pointed out that it is possible to arrange a series of calamitean cones, starting with forms which have the sporangiophore attached to the base of the dorsal segment, and ending with those which have it high up on the axis. It is interesting to note in this connection, that the number of vascular bundles in the axis of all calamitean cones yet examined is not greater than the number of sporangiophores, while the so-called sterile leaves are frequently twice as numerous as the vascular strands and consequently as the sporangiophores (Calamostachys). This feature, together with the fact that the sporangiophores were placed above and between the members of the reduplicated sterile whorl, and the fact that the nodes correspond in position to the latter (Williamson and Scott, Phil. trans. roy. soc., 1894, B., p. 902, 906), point to the conclusion that the pairs of sterile leaves were really dichotomously divided dorsal segments of sporophylls, of which the sporangiophores were the ventral segments, and in this feature (*i.e.*, dichotomy) resembled the foliage leaves of Archaeocalamites.

The morphological nature of the sporangiophore of Equisetum would appear in this connection to be problematical. Is it to be regarded as the result of the fusion of dorsal and ventral segments, such as has been shown to exist by Van Tieghem (Ann. sci. nat., bot., sér. 5, tom. 10) and Strasburger (Coniferen u. Gnetaceen) in the interesting peltate sporophylls of certain Cupressineae, or is it not rather to be considered as a ventral segment, the corresponding dorsal segment of which has become obsolete? If the former supposition is correct, there is no indication in the form of vestigial vascular bundles, in the axis of the sporangiophore, to indicate its morphological nature. We must await further knowledge of the cones of Archaeocalamites before attempting to decide this point, for these oldest known calamitean strobili had, according to the imperfect data at our disposal, the same external organization as those of living Equiseta. If it ever becomes possible to examine their internal structure, the sporophylls of this genus may prove to be analogous in organization to those of the Cupressineae referred to above, *i.e.*, composed of fused ventral and dorsal segments. In any case, there are many reasons for regarding the primitive type of sporophyll in the equisetaceous series as composed of a dorsal and a ventral segment, as Strasburger (*op. cit.*) considers to be the case in the analogous series furnished by the Coniferae.

Although the Sphenophyllales and Equisetales resemble one another so closely in their vegetative organization and in the structure of their strobili, a striking difference exists between the two groups, as Seward (Fossil plants, p. 388) has pointed out, in the structure of their vascular axes. In the former group, the central cylinder is protostelic, while in the latter it is cladosiphonic; but it has already been shown that these two stelar types may coexist within the same order and even within the same genus. In view, consequently, of numerous remarkable points of resemblance, the writer is of the opinion that the sphenophyllaceous and equisetaceous forms should be regarded as belonging to the same natural group, the former series being only more primitive than the latter. If this conclusion is correct, the phylum Equisetales must be made to include a new order, the Sphenophyllaceae, thus: —

Sphenophyllaceae.
Equisetales Calamitaceae.
Equisetaceae.

We may now turn to the question of the affinities of the Equisetales in the larger sense above indicated. It has already been pointed out that the siphonostely of the Filicales is phyllosiphonic, and that of the Lycopodiales, on the other hand, is cladosiphonic. The writer has reached the conclusion, for reasons indicated above, that the Equisetales are likewise cladosiphonic. Assuming that the occurrence of cladosiphony in the two groups is *prima facie* evidence of their relationship, it is necessary to add to this a number of other features of similarity before it can be considered as proved that the Lycopodiales and Equisetales are really somewhat closely allied.

Goebel (Bot. zeit., 1887) and Buchtien (*op. cit.*, p. 42) have both noticed the striking resemblance between the green gametophyte of *Lycopodium inundatum* and *L. cernuum* and that of the genus Equisetum; there are, in both cases, the same upright fleshy axis and the same characteristically numerous lateral lobes. Goebel (*op. cit.*) has noticed, too, that the archegonia of *L. inundatum* have the same relation to the lobes of the prothallus as those of Equisetum. The archegonia of Equisetum and Lycopodium are, moreover, alike, in that in both genera they are uniformly without the basal cell, which is found without exception in the archegonia of all the isosporous Filicales.

The antherozoids of the two groups differ in structure, those of the Lycopods being biciliate and moss-like, those of the Equisetaceae, on the other hand, being spiral and multiciliate. The embryo of *Equisetum hiemale*, as has been indicated in the earlier part of this essay, resembles that of Lycopodium in that root and shoot both originate from the upper (epibasal) region. But the resemblances are strongest in the sporophytic phases. Both groups are palingenetically microphyllous and have invariably strobiloid fructifications. In both these features they present a very marked contrast to the Filicales. Finally, both cohorts present the phenomenon of cladosiphony, and in this feature also are contrasted to the phyllosiphonic Filicales.

It may accordingly be assumed, if numerous features of resemblance are trustworthy indications of relationship, that the Equisetales in the larger sense indicated above and the Lycopodiales are closely allied, as indeed has already been suggested by Scott (Pres. address Brit. assoc., 1896, p. 15) in connection with the genus Sphenophyllum.

CONCLUSIONS.

The conclusions of this research may be stated as follows:—

1. The writer's investigation of the development of the vascular axis of the stem of the young plant, in a large number of representative vascular cryptogams and phanerogams, has led to the recognition of two primitive types of vascular axes *viz.*, the protostelic type consisting primarily of a single concentric bundle in the sense of De Bary, and the siphonostelic type, in which the vascular tissues from the very outset form a bundle-tube. Of siphonostelic axes there are again two types *viz.*, phyl-

losiphonic axes, in which the tubular vascular axis is interrupted by foliar lacunae occurring above the points of exit of the traces of the large leaves, and cladosiphonic axes, in which there are no foliar lacunae corresponding to the palingenetically microphyllous leaves, but which on the contrary are characterized by ramular lacunae appearing immediately above the departing traces of the branches. As regards the general morphology of vascular strands the writer, as a result of his study of development, returns to the standpoint of Sachs and De Bary.

2. The writer finds, with Goebel and Buchtien, that the gametophyte of the Equisetaceae, in its vertically-growing fleshy axis and its characteristically numerous thin lateral lobes, presents a detailed and striking resemblance to the green autotrophic species of prothallia of Lycopodium *viz.*, those of *L. inundatum* and *L. cernuum*. Further, the archegonium of the Equisetaceae resembles that of the isosporous Lycopods in being uniformly without the basal cell, which is invariably present in the archegonia of the isosporous Filicales. The embryo of *Equisetum hiemale*, the only species fully studied by the writer, agrees with those of Lycopodia described by Treub and more recently by Bruchmann, in the fact that both root and shoot originate from the upper (epibasal) region. Further, the sporophytic phases of the two groups also present a close agreement, since in both cases there are, invariably, microphyllous leaves and strobiloid fructifications.

3. In Archaeocalamites the internodal lacunae of the vascular cylinder occurred above the branches (as may be learned from Pl. 26 fig. 15), and the leaves were inserted at the nodes without lacunae in the course of the continuous vascular strands. This genus was consequently cladosiphonic and in this respect resembles the higher Lycopods. During the phylogenetic development of the Calamites the segments of the stem were gradually rotated on each other, as has been shown by Stur, and as a consequence of this process the ramular lacunae were ultimately shifted, so as to coincide with the leaf-traces, but the latter give evidence of their true affinities, even in the modern Equiseta (Pl. 26, fig. 16), by the fact that their apparent foliar lacunae are separated from them by the whole depth of the nodal wood. Moreover, the writer's examination of the development of the young stele in Equiseta shows, that it is primitively tubular and not, as Van Tieghem suggests, dialydesmic. The data of phylogeny, ontogeny, and anatomy consequently all favor the view that the Equisetaceae are, like *Selaginella laevigata* and *Lepidodendron harcourtii*, cladosiphonic, and there are thus additional reasons for regarding the Lycopodiales and Equisetales as closely allied.

4. The Sphenophyllales are the protostelic ancestors of the Equisetales and agree with them closely in all particulars, except the structure of their stele. But as has been pointed out, protostely and siphonostely may occur in different genera of the

same family, and even in different species of the same genus. The writer consequently is of the opinion, that the Sphenophyllales cannot any longer, on that ground, be regarded as a separate phylum, but must be included with the Equisetales as an additional order, thus: —

	Sphenophyllaceae.
Equisetales	Calamitaceae.
	Equisetaceae.

5. The branches of the Calamites did not, as has been stated in recent years, arise above the nodes, but, like those of the Equisetaceae, originated either more or less exactly from the center of the ring of nodal wood, or from its lower border.

6. The more conspicuous series of nodules on the medullary casts of the Calamites are not impressions of Williamson's infranodal canals, but on the contrary of the short cylindrical medullary cavities of modified rhizophorous branches, homologous with those of living Equiseta.

7. Nodal periderm is present in certain species of Equisetum and is comparable to that described by Williamson and Scott as occurring in the nodal diaphragms of Calamites.

This investigation was completed in the Cryptogamic laboratory of Harvard university, and the writer offers his best thanks to Dr. W. G. Farlow and Dr. Roland Thaxter for their courtesy and advice. He is also under obligations to Dr. G. L. Goodale for material and the use of photographic apparatus belonging to his department, and to Dr. B. L. Robinson for cones of a large number of species of Equisetum from the collections in the Gray herbarium.

EXPLANATION OF PLATES.

PLATE 26.

Fig. 1. Young archegonium of *Equisetum hiemale*.

Fig. 2. Older archegonium of *E. hiemale*.

Fig. 3. Older archegonium of *E. hiemale*.

Fig. 4. Nearly ripe archegonium of *E. hiemale*.

Fig. 5. Nearly ripe archegonium of *E. arvense*.

Fig. 6. Young embryo of *E. hiemale*

Fig. 7. Older embryo of *E. hiemale*.

Fig. 8. Still further advanced embryo of *E. hiemale*.

Fig. 9. Young sporophyte of *E. hiemale*.

Fig. 10. Older sporophyte of the same species.

Fig. 11. Advanced sporophyte of *E. hiemale*.

Fig. 12. Young sporophyte of *E. limosum*.

Fig. 13. Older sporophyte of the same species.

Fig. 14. Diagram showing the relation of the leaf-traces to the nodal wood in *E. hiemale*. *n. w.* nodal wood; *e.* endodermis; *p. t.* protoxylem; *l. t.* leaf-trace.

Fig. 15. Diagram of the node of *Archæocalamites*. *l.* leaf-traces; *b.* branches.

Fig. 16. Diagram of the node of Equisetum. *l.* leaf-traces; *b.* branches.

Fig. 17. Surface of a Calamite showing the scars of leaves, branches, and root. For explanation see page 181.

PLATE 27.

Fig. 1. Stele of *Selaginella laevigata* showing the origin of a branch. ×25.

Fig. 2. Stele of the same species below the point of origin of a branch. ×25.

Fig. 3. Stele of *Lepidodendron harcourtii* at the point of origin of a branch. ×25. See page 161.

Fig. 4. Tangential view of the bundles at the node of a Calamite, copied from Williamson. See page 163.

Fig. 5. Tangential view of the bundles at the node of a Calamite, copied from another of Williamson's figures. See page 163.

Fig. 6. Tangential view of the bundles at the node of a Calamite, copied from a figure of Williamson and Scott. See page 164.

PLATE 28.

Fig. 1. Tangential view of the bundles at the node of a Calamite, copied from Renault. See page 165. (In this figure there are leaf traces, *f*, only at alternate strands, a state of affairs not uncommon in the Calamites).

Fig. 2. Transverse section of a young [illegible] stem of *Equisetum limosum*. ×200.

Fig. 3. Transverse section of the stem of *E. hiemale* in the nodal region. *a.* branch; *b.* a root. ×25.

Fig. 4. Nodal organ of *E. hiemale*. ×200.

Fig. 5. Transverse section through the node of *E. silvaticum*. *a.* nodal organs; *b.* roots; *c.* a branch; *d.* leaf-traces; ×25.

Fig. 6. Node of *E. arvense*. *c.* branches; *d.* leaf-traces. ×25.

PLATE 29.

Fig. 1. Transverse section of a node of *Equisetum limosum*. *c.* branch; *d.* leaf traces; *b.* rhizophoric organs. ×25.

Fig. 2. Tangential section of the node of *E. hiemale*. *c.* branch; *l.* leaf traces; *l.* vallecular lacunae. ×25.

Fig. 3. Deep tangential section of the node of *E. hiemale*. *c.* branch; *l.* vallecular lacunae. ×25.

Fig. 4. Deep tangential section of the node of the rhizome of *E. hiemale*. *c.* a branch; *l.* vallecular lacunae. ×25.

Fig. 5. Radial section through an aerial node of *E. hiemale* at the point of origin of a branch. *d.* nodal diaphragm; *n.* nodal wood; *c.* the branch; *r.* roots; *k.* nodal shoot of the branch. ×25.

Fig. 6. Radial section of a terrestrial node of *E. hiemale* at the point of origin of a nodal bud. *d.* nodal diaphragm; *n.* nodal wood; *c.* nodal bud; *r.* root. ×25.

PLATE 30.

Fig. 1. Radial section of a terrestrial node of *Equisetum hiemale* at the point of origin of a large vertical branch. *d.* nodal diaphragm; *n.* nodal wood; *c.* branch; *r.* root. ×25.

Fig. 2. Radial section of a node of a terrestrial branch of *E. silvaticum*; lettering as in Fig. 2. ×25.

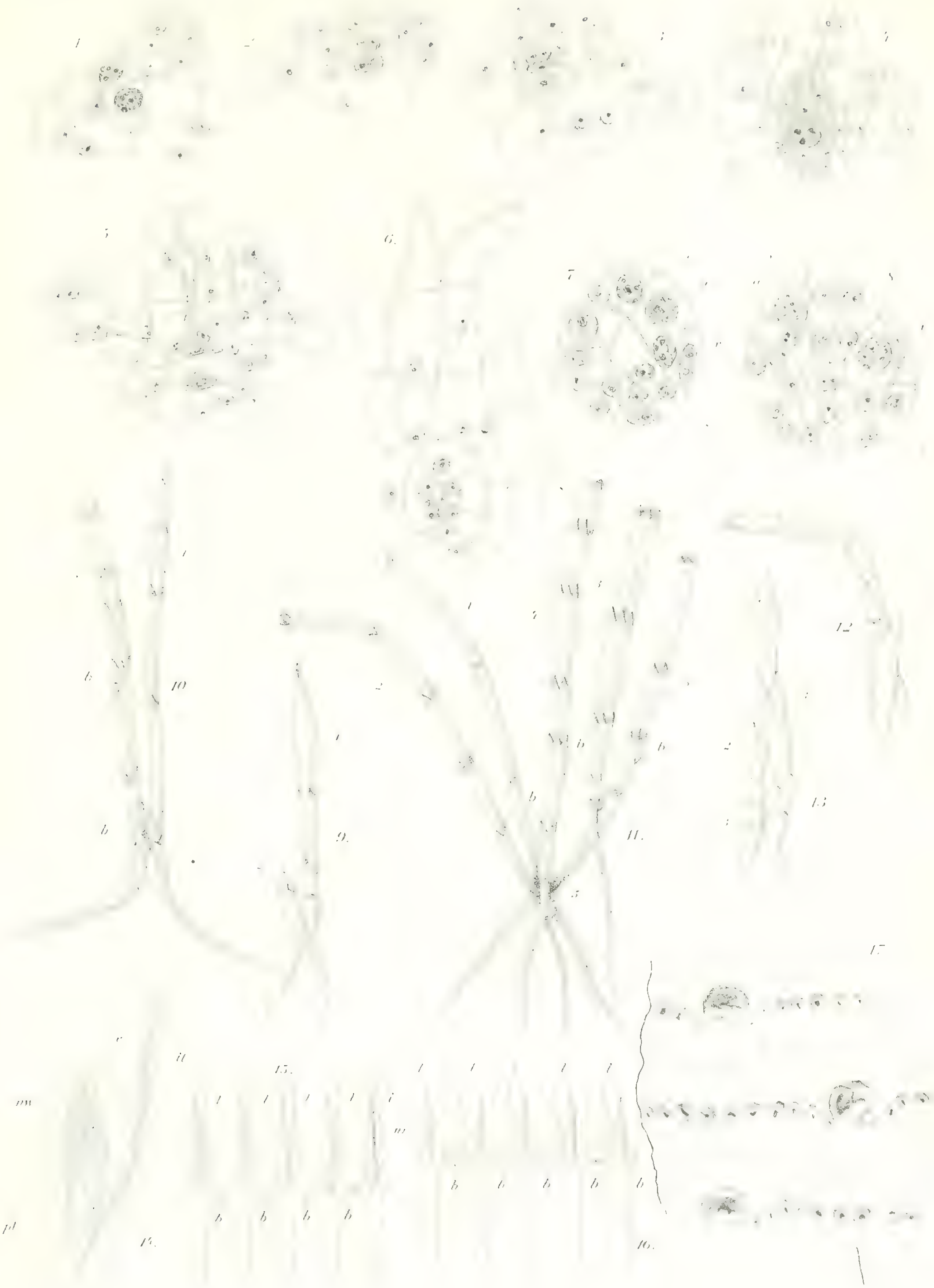
Fig. 3. Course of the bundles in the cone of *E. arvense*. ×4.

Fig. 4. Tangential section passing through the leaf-trace of *E. hiemale* and showing its mode of origin from the protoxylem of the internodal bundle. *px.* protoxylem; *mx.* metaxylem; *lt.* leaf-trace; *n.* nodal wood. ×200.

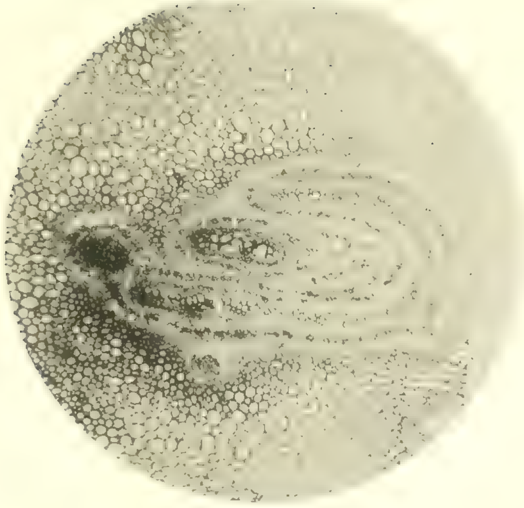
Fig. 5. Section through the nodal diaphragm of *E. hiemale*. ×200.

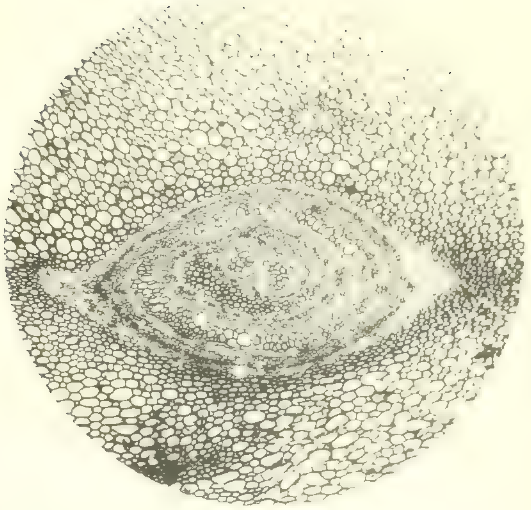
Fig. 6. The surface of a Calamite, copied from Weiss, showing four whorls of attached leaves a nda single row of scars of fallen branches. The latter have scars of fallen leaves along their lower margin.

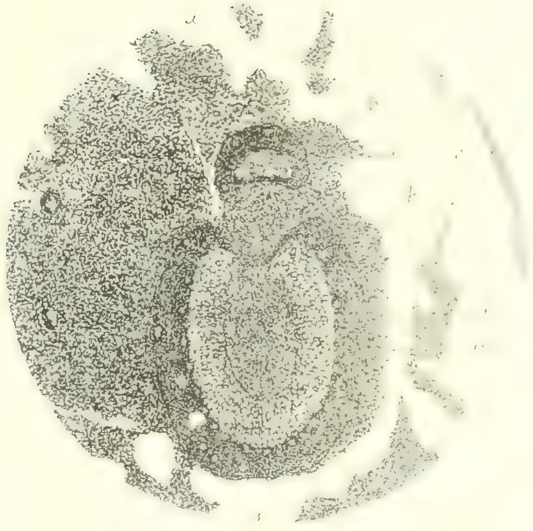
Printed, April, 1899.



JEFFREY, EQUISETUM.







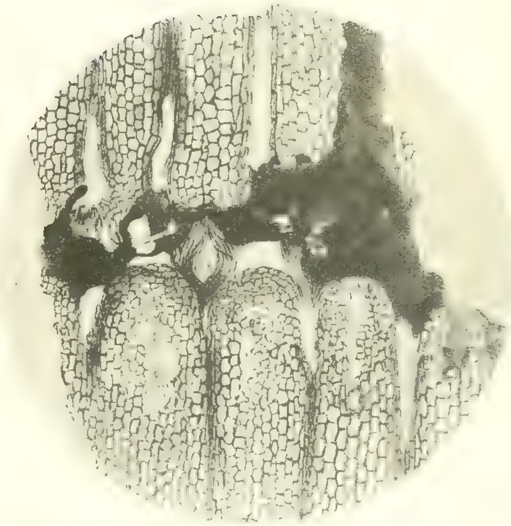
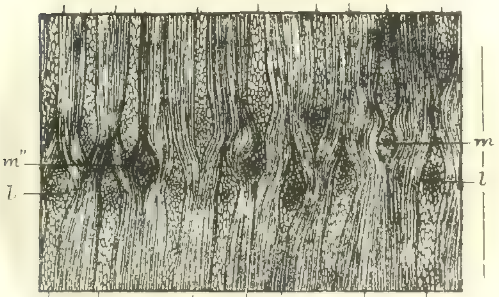
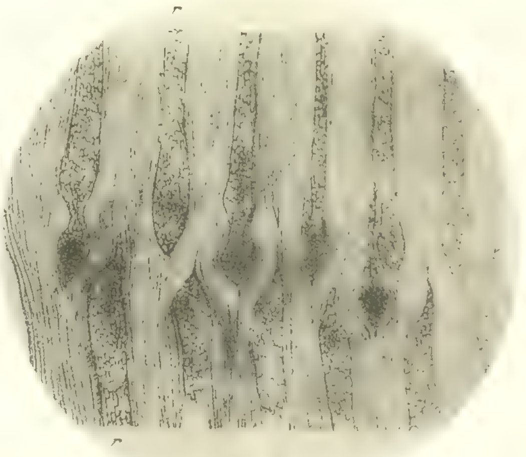


Fig 23

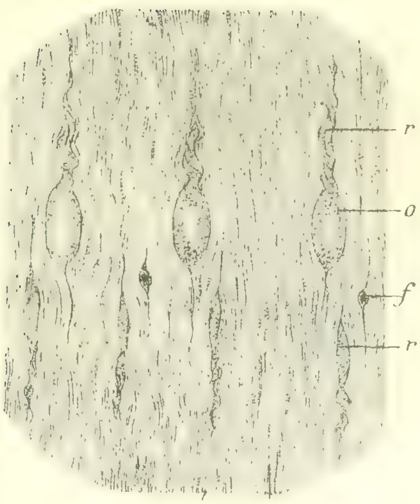


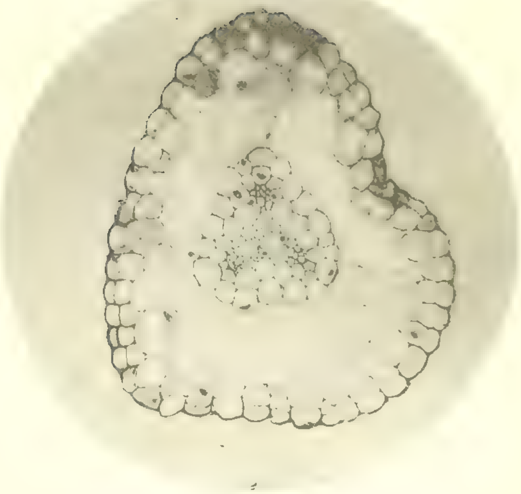
5



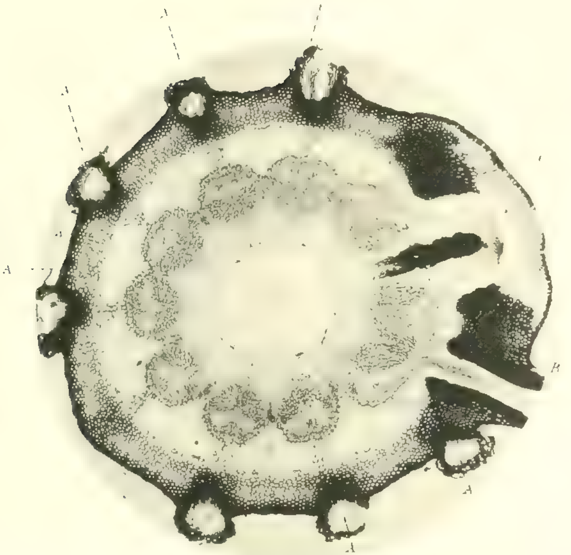
6

1

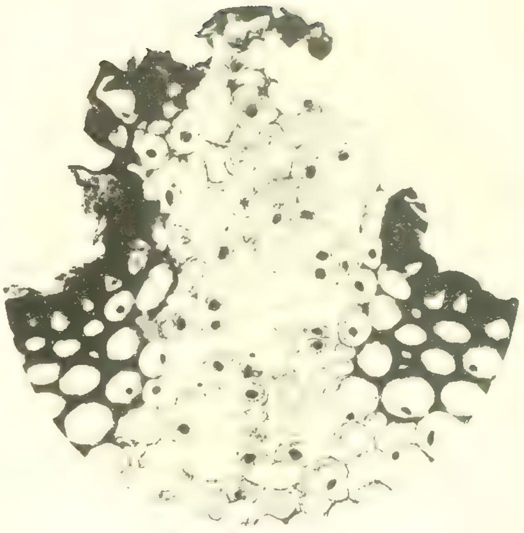




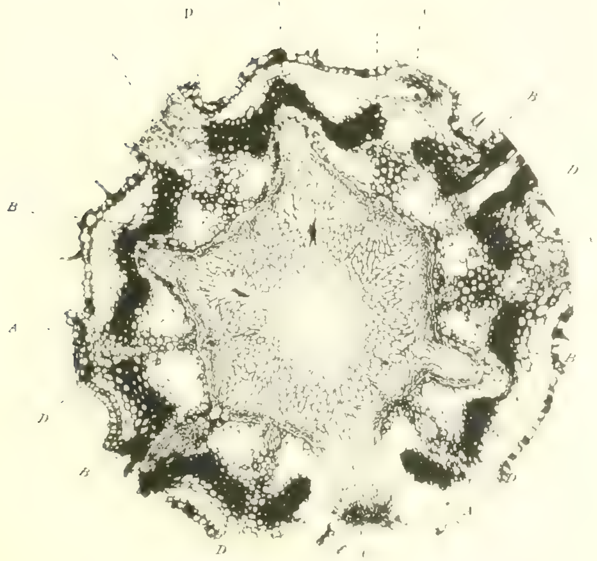
2



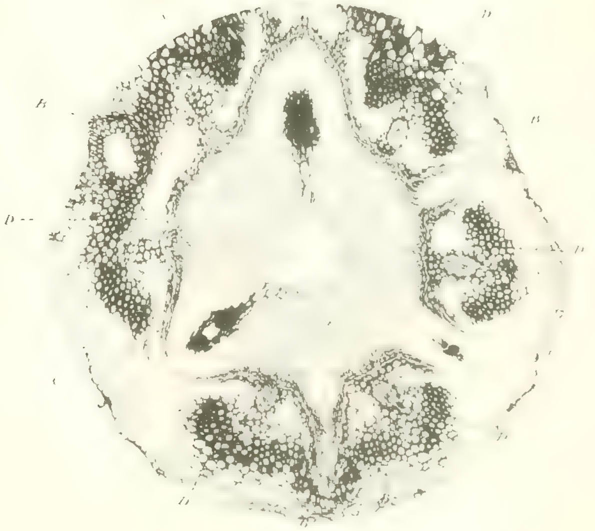
3

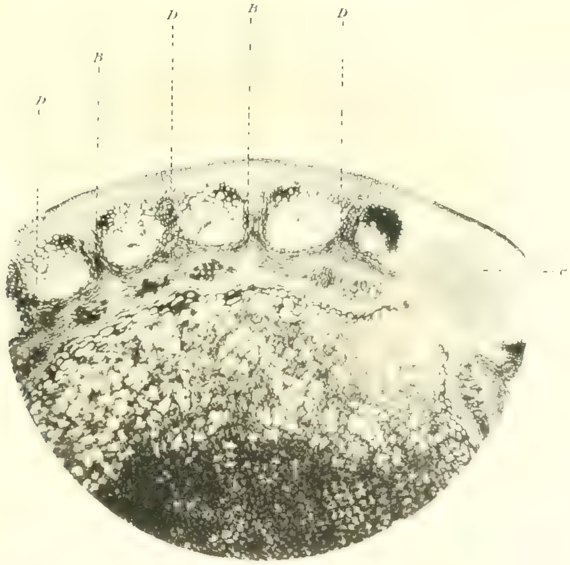


4

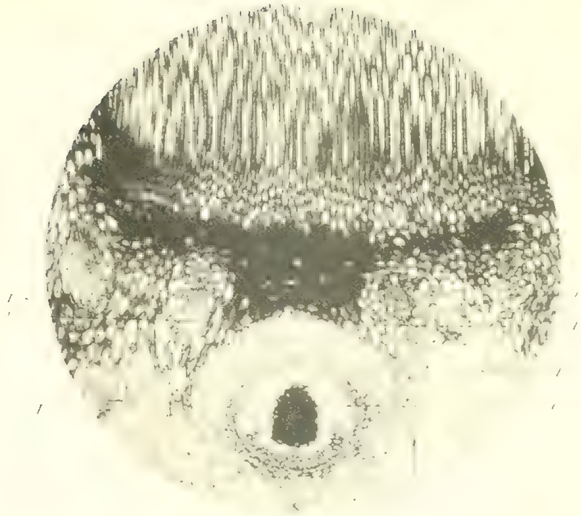


5

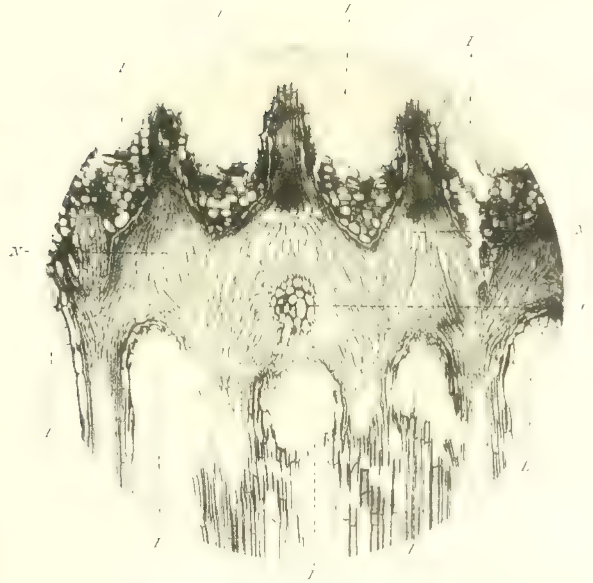




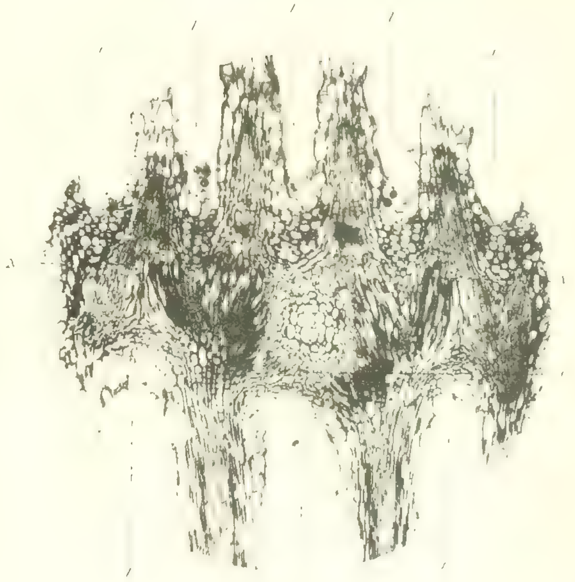
1



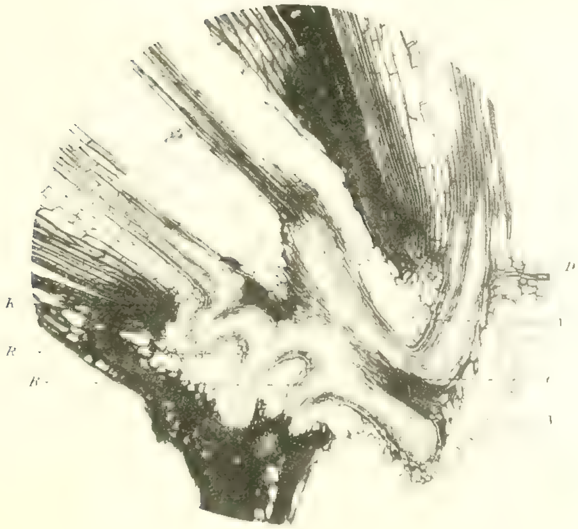
2



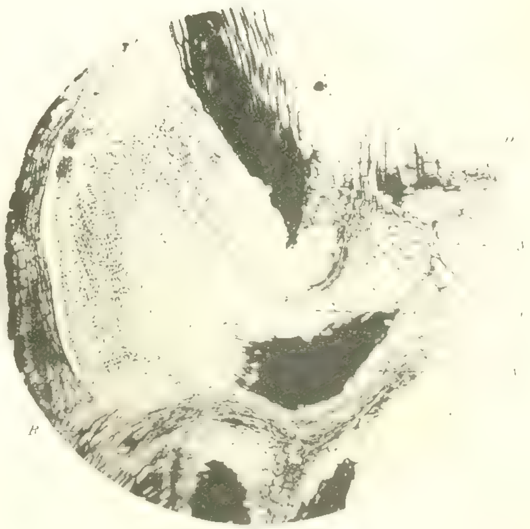
3



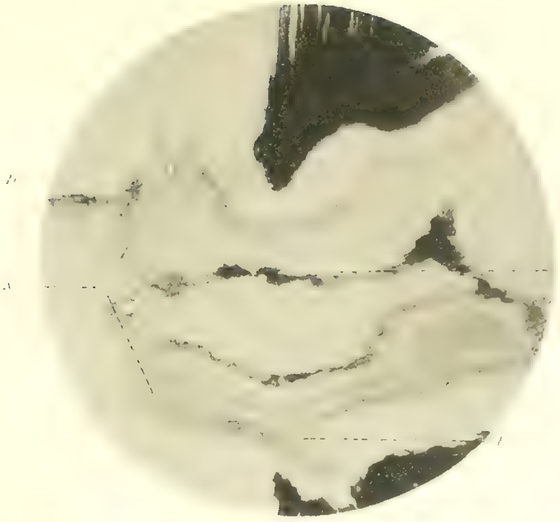
4

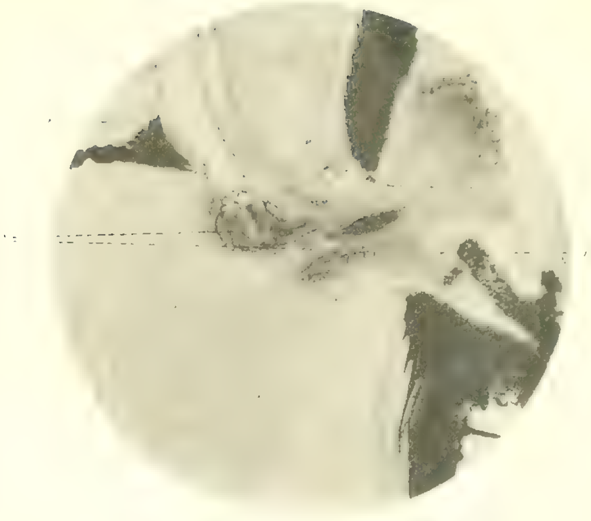


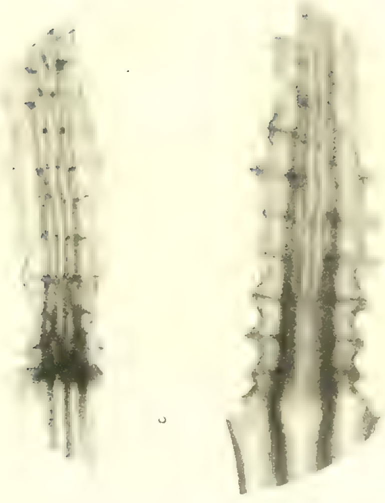
5

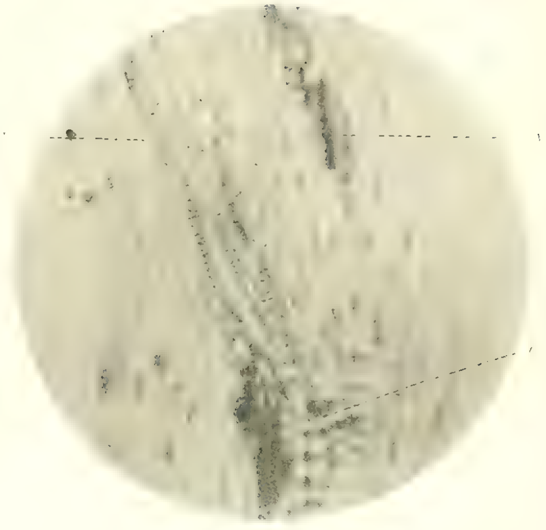


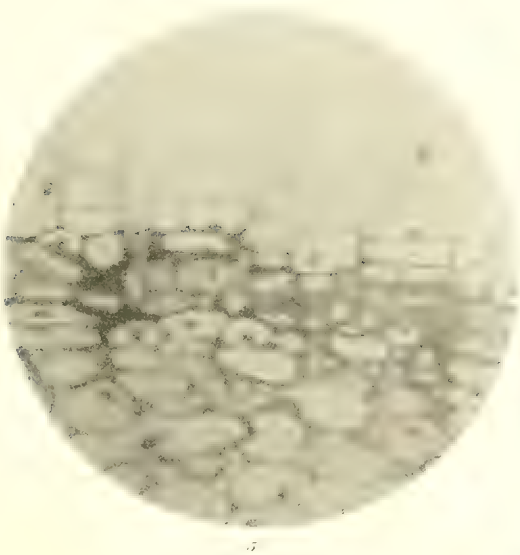
6



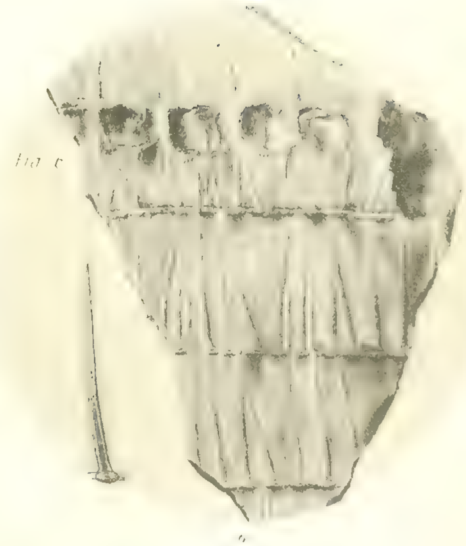








5



6

6. THE ANATOMY AND DEVELOPMENT OF CASSIOPEA XAMACHANA.[1]

BY ROBERT PAYNE BIGELOW.

INTRODUCTION.

During the summer of 1891 the Marine Laboratory of the Johns Hopkins University was stationed in the Island of Jamaica. It was at Port Henderson, — a little hamlet situated at the west side of the mouth of Kingston Harbor, at the point where the Salt Pond Hill, eight hundred feet high, descends to the salinas and mangrove swamps surrounding the mouth of the Rio Cobre. On the other side of the hill, and to the south of it, there is a considerable body of salt water, known as the Great Salt Pond. It is completely separated from the sea, but only by a beach of sand, which at its narrowest part is not more than a few rods in width; and it is said by those who live near that in times of storm or freshet this barrier may be broken through.

One morning in June Dr. G. W. Field was hunting birds along the seaward shore of this pond, and came upon a little bay that forms a deep indentation in the barrier and is connected with the pond by a narrow inlet. The bay is overhung by low cashaw and mangrove trees. At one side is a sunny sandy spot where a crocodile had made its bed, and a fresh zigzag mark showed where it had recently slid into the water. A school of fish was circling about in the clear water, and barnacles and sea-anemones spread their tentacles from the submerged roots of the mangroves, while the bottom at the inner end of the bay was completely carpeted by a colony of beautiful rhizostomatous medusae.

A few very small specimens might be seen swimming about, but most of the medusae, especially the larger ones, would not ordinarily leave the bottom. They lay there upon their backs, with their voluminous, branching mouth parts spread out over their discs, which were motionless, except for occasional flaps of their margins. If any of these animals were disturbed, they would, however, swim about like ordinary medusae; but before long they would settle down again and assume their usual attitude upon the bottom.

---

[1] An earlier draft of this paper was accepted in May, 1892, by the Board of University Studies in the Johns Hopkins University as a thesis for the Degree of Doctor of Philosophy. During the years 1891–92 and 1892–93 I held the Adam T. Bruce Fellowship in the Johns Hopkins University, and was thus enabled to make a second journey to Jamaica. Publication has been delayed in order that the results of this journey might be incorporated in the paper, and it is hoped that the greater accuracy and completeness thus obtained have added materially to its value.

Within this limited area there were countless numbers of them, and in many places they were so thickly spread that their margins touched upon all sides, or even overlapped.

The spectacle presented by this collection of medusae was truly marvelous; and in order to show something of it to the rest of us, Dr. Field gathered a pailful of specimens and brought them to the laboratory. Upon examination they were all found to belong to a single new species of Cassiopea, — a genus of which only one species was known to occur outside of the Red Sea, Indian Ocean, and southwest Pacific;[1] and this pailful, taken up at random, contained both adults and young in various stages of growth.

Professor Brooks made drawings of some of these, and then I made a visit to the Salt Pond to obtain more of the young medusae, and at the same time I collected submerged bits of wood and stems of plants. My hopes were more than realized when, upon examining these objects in the laboratory, I found them thickly studded in places with scyphistomas in various stages of development. I was particularly delighted when I noticed in one of the largest larvae certain glistening spots in the bases of the tentacles and found, on putting them under the microscope, that they were unmistakably masses of calcareous bodies that would form part of the marginal sense organs of the adult. They excited my interest, especially as I had been studying the development of these structures in Discomedusae ('**90**), and had been unable hitherto to obtain the early stages.

After this discovery I began, with the advice of Professor Brooks, to make a careful study of this species, with the intention of carrying the investigation of its anatomy and development as far as the limited amount of time at my command would allow. Preliminary accounts of my results were published in 1892 (Bigelow, '**92**, *a*, *b* and *c*). In the spring of 1893 I had another opportunity to visit Port Henderson with a party from the Johns Hopkins University, and was able to make important additions to my earlier observations.

During the first visit to Jamaica I was unable to find Cassiopea outside of the one locality that I have described, and, although both the adults and the young in nearly all stages were present at this place in such great numbers, searches for males and for females with ripe eggs were equally fruitless. The great abundance of young and the range in their apparent ages was, therefore, surprising, until I found that the scyphistomas were multiplying freely by budding, in a manner to be described later on. During my second visit I found this species as abundant as ever in this locality, and I also found a number of adult specimens in several of the small shallow lagoons among the mangroves in the rear of Port Royal. But these were all females, and it was still impossible to obtain males or eggs that would develop.

---

[1] Although Fewkes ('**82**) identifies his *Cassiopea frondosa* Lamarck, of Key West and the Tortugas, with *Polyclonia frondosa* Ag., it is nevertheless a true Cassiopea, not a Polyclonia.

Full-grown medusae could be kept in good condition in aquaria for a number of days, and could be kept alive for weeks; while the young medusae and scyphistomas would thrive there an indefinite time, if there were a little pond ooze at the bottom of the aquarium and the water were changed twice a day. Indeed the growth and multiplication of the scyphistomas would proceed actively under these conditions. By keeping the larvae in shallow dishes I was able to watch the whole course of non-sexual development; but the development from eggs remains unknown to me because of the impossibility of finding any that would develop. It was not until a few days before we left Jamaica in 1891 that I discovered the habit that the very young free-swimming larvae have of hiding beneath the bits of bark and the like to which the scyphistomas in the aquarium were attached, and therefore the greater part of my work on the early stages of development was done during the second expedition.

After a few words concerning technique I shall begin with a systematic description of the species, followed by an account of the anatomy of the adult, and the remaining part of the paper will contain what I have learned of the development from the observation of the living animals while in Jamaica, and by the study of sections of preserved material, carried on chiefly at the Biological Laboratory of the Johns Hopkins University, but in part also at the Marine Biological Laboratory of Woods Hole and at the Biological Laboratory of the U. S. Fish Commission in the same place.

I wish to express my thanks to Professor W. K. Brooks for the advice and encouragement that he gave me while I was doing this work as one of his students, and I am also indebted to Professor C. O. Whitman, to the Hon. George M. Bowers, and to Professor H. C. Bumpus for the many courtesies received while at Woods Hole.

TECHNIQUE.

For the preservation of the very young larvae a one quarter saturated solution of picric acid, with 2% of sodium chloride added, gave good results. Erlicki's fluid with the same addition, and ½% osmic acid followed by Erlicki's fluid, did fairly well for scyphistomas, but the best specimens obtained were those killed in the following mixture:

10% solution copper sulphate	100 c. c.
saturated solution corrosive sublimate	10 c. c.

As soon as they were killed, the specimens were placed in 5% bichromate of potassium and left there until hardened, after which they were washed in 35% alcohol containing a trace of hydrochloric acid and preserved in 70% alcohol. Excellent preparations of the medusae were obtained by this same method, and Flemming's fluid also gave good results.

SYSTEMATIC PART.

Genus **Cassiopea** PÉRON and LESUEUR (*1809*). — This genus, as limited by Haeckel ('**80**), may be defined as follows: Discomedusae without tentacles and without a central mouth opening; provided, instead of the latter, with numerous oral funnels attached to the ventral, or axial, side of the *eight oral arms*, which are *pinnately or trichotomously branched*, have a *subcylindrical*, or *subconical*, *gelatinous support continuous to the tips of the principal branches*, are provided with *numerous club-shaped vesicles* among the oral funnels, and are without appendages on the dorsal, or abaxial, side; also with four interradial gonads in the aboral wall of the four separate subgenital cavities; *sixteen marginal sense organs* (*rhopalia*); and *thirty-two radial canals* connected by a network of anastomosing branches.

For the sake of clearness this definition is made to include the characters of the family Toreumidae Haeckel, to which this genus belongs, and the purely generic characters are italicized.

Cassiopea xamachana.[1]

Cassiopea xamachana BIGELOW, Zool. Anzeiger, no. 393, 1892, pp. 212–214.

(?) *C. frondosa* FEWKES, Bull. mus. comp. zool., vol. 9, no. 7, 1882, pp. 254–259.

Diagnosis. — A Cassiopea with a disc-like umbrella, concave on the aboral side; when regular, with eighty short and obtuse marginal lobes separated by deep grooves on the surface of the exumbrella (in each of the sixteen parameres three velar lobes between two ocular ones); white markings on the exumbrella, consisting of a circular band with a diameter somewhat greater than that of the concavity, within this sixteen oval or eliptical spots lying in the radii of the rhopalia, and on the outer side eighty marginal spots, one for each marginal lobe; oral arms rounded and slender, never angular, exceeding the radius of the umbrella by at least one half of its length, and bearing nine to fifteen primary branches which are, in turn, copiously branched, giving the whole appendage a spatulate outline; very numerous small oval vesicles attached at the axils of the small branches and thickly massed upon the oral disc of adult females, and many small and a few large, flattened, linear vesicles attached one at the axil of each of the larger branches and to the canals on the oral disc, the thirteen largest vesicles being one at the axil of the largest branch on each arm and one at each junction of the canals on the oral disc: oral funnels entirely wanting on the oral disc in adult females, but present in immature specimens.

---

[1] This name, suggested by Professor Brooks, must stand as printed in the preliminary description of the species, according to the current rules of nomenclature, followed by the Boston Society of Natural History. But it should have been written *xamaycana*, from *Xamayca* (the *x* is pronounced like *ch* in the German *ach*), the Indian name for the island of Jamaica, as written by the early Spanish historians (see Herrera, Novi orbis pars duodecima, sive descriptio Indiæ occidentalis, 1624; also Encycl. Brit., 9th ed., article, Jamaica). The form *Xaymaca* given by Bridges, Annals of Jamaica, 1827, and followed by several subsequent authors, is probably a misprint.

Special description. — A detailed account of the anatomy of this species will be given in the anatomical portion of this paper. It is intended here to call attention merely to the features that distinguish our species from its nearest allies. *Cassiopea xamachana* resembles very closely two medusae that inhabit the Red Sea and Indian Ocean, *Cassiopea andromeda* Eschscholtz and *C. polypoides* Keller ('**83**), but it seems, nevertheless, to be distinct from either.

Upon comparison with the descriptions of *Cassiopea andromeda* given by Tilesius ('**29**), Haeckel ('**79**), and Vanhöffen ('**88**), and with the figures of Tilesius ('**29**) and Forskål (**1776**), *C. xamachana* appears to differ from this species in the following particulars: The exumbrella is not merely flat, but is concave; besides the ninety-six white spots on the exumbrella, there is a broad circular band of white more or less connected with all of the marginal spots (Fig. 35), the oral arms are more thickly branched and are longer, exceeding by one half to two fifths the radius of the umbrella, instead of being only one third longer; moreover the arms have none of the flattened appearance figured by Tilesius and mentioned by Haeckel.

C. xamachana differs from *C. polypoides* in having more slender oral arms, with five to seven pairs of branches instead of three, and with fewer very large vesicles, and these apparently not so large and always flattened. The color pattern in the two species is nearly the same, except that in *C. xamachana* the three white spots on the three velar lobes of each paramere are seldom widely separated from the circular band of white. The colors in the pattern, however, differ considerably in the two species. The ground color in *C. xamachana* is never light brown, but is always much darker, a greenish brown, usually with a distinct shade of blue on the subumbrella. The large oral vesicles are never sky-blue, rose-colored nor white, but are yellowish green, often with a bluish green stripe; and, while the margins of the oral funnels are deep brown, they are always fringed with the white digitella.

C. xamachana is easily distinguished from *C. ornata* Haeckel by the presence of large oral vesicles and by the more extensive branching of the arms; and it differs from *C. mertensii* Brandt ('**38**), *C. depressa* Haeckel ('**80**), and *C. picta* Vanhöffen ('**88**), in the number of marginal lobes on the umbrella. *C. ndrosia* Agassiz and Mayer ('**99**) differs also in number of marginal lobes and in coloring. Fewkes ('**82**) has described a medusa from Key West and the Tortugas under the name "*Cassiopea frondosa* Lamarck," which he regards as identical with *Polyclonia frondosa* Agassiz. From the description given by

Fewkes it is impossible to identify his species positively. But a comparison of his figures with living specimens of both sexes of *P. frondosa* shows at once that the two species are distinct; while a comparison with *C. xamachana* shows so close a resemblance that I am inclined to think that Fewkes has discovered one of the varieties of our species, described in the next section. Not only is *P. frondosa* perfectly distinct from *C. xamachana*, but I think we are justified in retaining the former, for the present at least, in a separate genus; and there can be little doubt that Lamarck's *Cassiopea frondosa* dwelling in the "Ocean of the Antilles" with its "*margine decem-lobata*" is none other than Agassiz's *Polyclonia frondosa*. Therefore, even if it should be proved that the form described by Fewkes is the same as the subject of the present memoir, the name that I have given to it will hold, nevertheless, as the designation of the species.

Variations. — If we compare the average dimensions of various organs, expressed in thousandths of the diameter, with the maxima and minima, as may be done by examining the third, fourth, and fifth columns in Table 1, p. 201, it becomes evident that there is a very considerable amount of variation in the relative size of parts of *C. xamachana*.

In the oral arms, not only does the relative size vary, but the number and the arrangement of the branches are both variable. Moreover this variability exists between the different individuals. In nineteen specimens examined the maximum number of branches found on one arm was sixteen, the minimum nine, and the greatest difference on any one individual was four.

The most striking variations in *C. xamachana*, however, are to be found in the structures at the margin of the umbrella. These are highly variable in this species, and have been found to be variable, although to a less extent, in other medusae. It is unfortunate, therefore, that in his beautiful systematic work on the medusae Haeckel should have found himself forced to distinguish the genera chiefly by differences in the marginal structures. He himself notes the variability in the number of parameres of *Polyclonia frondosa*. Agassiz and Mayer ('99) found in one specimen of *C. ndrosia* eighteen rhopalia, and in another twenty-two.

The number of rhopalia was counted in twenty-seven specimens of *C. xamachana*. Of these ten were found to have sixteen, the typical number for the genus, and twelve had more than sixteen, three having seventeen, and three more, eighteen. The largest number on one individual was twenty-three. There were five specimens with fewer than sixteen rhopalia, but only two had less than fifteen, and both of these showed correlated abnormalities in the mouth parts and subgenital cavities. One had fourteen rhopalia, four oral arms, and two subgenital cavities and gonads. The other had ten rhopalia, only five oral arms, with three oesophageal canals leading from the stomach to the canal system of the arms, and three normal subgenital cavities and one very small vestigial one (Fig. A.).

Redundancy of mouth parts is not nearly as common as of the marginal structures. Only two cases were observed. One specimen with an additional pair of oral arms in one interradius had seventeen rhopalia. The other had eleven arms, with five subgenital spaces and gonads, and this one had twenty-two rhopalia. On the other hand, five specimens were found with twenty or more rhopalia, and perfectly normal mouth parts.

It will be seen, then, that the number of rhopalia, which has been taken as the principal generic character in the group, is a highly variable one. The number of marginal lobes in each paramere has been taken as one of the principal specific characters, and this is, likewise, highly variable. The variation consists principally in the interpolation of a small secondary lobe between two typical ones. Even in a regular and typical specimen, such as is shown in Fig. 35, the position that would be taken by these secondary lobes is indicated by small ridges on the dorsal surface. A specimen with a large number of rhopalia is as likely to have the marginal lobes in each paramere arranged typically as one having a smaller number. Conversely, a specimen with fifteen to seventeen parameres is as likely as not to vary from the typical form. The variation may consist in the addition of two secondary lobes in the paramere, the addition of four lobes, or in a quite irregular arrangement ; and this modification may affect all of the parameres alike or only a portion of them.

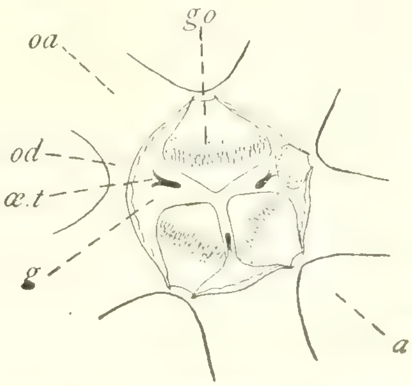


Fig. A. Section through the stomach of a specimen with only 10 rhopalia and 5 oral arms, to show the abnormal arrangement of gonadia and oesophageal canals. In the region marked *a* the margin of the umbrella presents a wide space in which there are no rhopalia. *go* = gonad. For explanation of the other lettering see Explanation of Plates.

Throughout all of these modifications of the margins there is manifested a constant regard, as it were, for the symmetry of the parts. It is very seldom that an additional rhopalium appears as if attached fortuitously in some irregular way. Almost always either it is in the midst of an entirely new paramere or else there is a distinct line of symmetry running between two adjacent rhopalia that evidently correspond to an originally single one. In other words, a paramere has been incompletely doubled, and the two parts are bilaterally symmetrical to one another. We find all degrees of this doubling in the adult from a double-headed rhopalium[1] to two complete parameres, and the same process may be seen in the forked tentacles frequently found in the larvae (Figs. 14 and 21, *x*). With the exception of the forked tentacle and the double-headed rhopalium, these stages of duplication are well represented at *u*, *w*, *x*, *y* and *z* in Fig. 30.

The radially arranged stripes and spots on the exumbrella, which, with a circular band, form the color pattern described in the next section, vary in number with the rhopalia and marginal lobes. But when two rhopalia are close together there may be only one corresponding rhopalial stripe, and it will then occupy a position intermediate between the two. For example, in the specimen mentioned before as having only ten rhopalia, two of the rhopalia were very close together and there was but one rhopalial stripe corresponding to them. The other rhopalia were evenly spread, except that they were absent from one rather wide section of the circle. The rhopalial stripes, nine in all, were placed in a corresponding manner, and were absent from the corresponding area.

There is also a wide degree of variation in the extent of fusion between the circular band and the marginal spots. The spots on the velar lobes are usually not fused to the circular band in young specimens, and they frequently remain distinct in adults. It was found, however, that this is more usually true of specimens from the Salt Pond than of those from Port Royal. I thought that I could see, also, correlated differences in the sizes of certain of the mouth parts, and I was thus led to inquire if there were a division here of the species into two races. For this purpose Table 2, p. 201, was constructed. From this it will be seen that the specimens from the Salt Pond (var. *A*) have on the average longer oral arms and shorter vesicles than the ordinary specimens from Port Royal (var. *B*), while the stomach is of the same size in the two groups. Whether these slight differences are in any way connected with the probable difference in density of the water in the two localities, experiment alone can determine.

In the third column of this table dimensions are given of some specimens from Port Royal (var. *C*) that are so different from the rest that they might be regarded as of a distinct species.[2] Suspicion of their being merely sports is aroused, however, by the fact that only two specimens (female) were found living among a large number of the usual form.

The most striking peculiarity of these two specimens was the great number (forty to fifty) of uniformly large oral vesicles, two to four centimeters in length, scattered over the whole extent of the mouth parts. Among them the central, radial, and primary vesicles were hardly distinguishable, although so easily recognized by their greater size in the typical form of the species.

---

[1] Fewkes, ('82) has observed similar double-headed rhopalia, and it is on account of the variability of the marginal structures that he regards Polyclonia as merely an abnormal Cassiopea.

[2] It is possible that this variety may be the same as *Cassiopea frondosa* Lamarck of Fewkes, although his figures do not show any large vesicles on the proximal parts of the oral arms.

Another peculiarity was a projection of the mesogloea on the oral side of each subgenital osteum, so that the interradial diameter of the oral disc was considerably longer than the radial diameter, as shown in the table. These specimens presented also some peculiarities of coloring, which will be noted in the next section.

Color. — The coloring of this semi-transparent animal consists of certain white markings, together with shadings of subdued tints of brown, green and blue, that are often very beautiful.

If we turn the aboral side (Fig. 35) of the medusa toward us we find often a brownish band encircling the disc at the periphery of the concavity and shading off gradually on both sides. Deeper within the mesogloea there is a much wider white circular band extending under the brownish one; and white bands, or spots, extend in a radial direction outward from this along the marginal ridges. There is one spot to each ridge, and it reaches nearly to the tip of the marginal lobe. The bands on the rhopalial lobes are interrupted, however, by a roughly circular, transparent area over each rhopalium; and in many specimens, especially young ones, the interrhopalial (velar) spots are not fused with the circle. On the inner side of the circular band of white there is a circle of large white spots, "rhopalial spots," or stripes, that lie deep in the substance of the exumbrella and are visible through the mesogloea, one in the radius of each rhopalium. The spot is elliptical in outline, and extends from the white band to a point about two fifths of the distance between the periphery of the concavity and the edge of the stomach. These spots, while usually continuous with the band, like the marginal spots, are not always so.

At the centre of the umbrella the stomach and subgenital cavities may be seen through the mesogloea as a reddish brown circular area with a diameter of about one fourth of the total diameter of the disc; while surrounding the stomach there is a deep blue halo with points that extend outward between the last-mentioned bands of white.

Now if the animal be allowed to return to its usual position, the subumbrellar surface will be found to be pretty evenly stippled by the greenish brown cells in the mesogloea. Apparently beneath this stippling there is a blue pigment forming a circle around the margin of the stomach and extending outward in broad bands, one along each interrhopalial radius, nearly or quite to a large, more or less distinct patch of blue, that lies close to the margin between every two rhopalia. The radial canals, and the fine, connecting network of tubes, appear as rather indistinct, opaque, white lines.

The mesogloea of the oral arms is transparent and colorless, except for an opaque white stripe beneath the dorsal surface of each arm, of the same character as the white markings of the umbrella. There is a similar stripe on the dorsal side of each of the larger branches which may, or may not, be continuous with the stripe on the main stem. The bases of the oral funnels are of a delicate blue color, which often extends to the brachial canal. The margin of each funnel is a deep brown, that shades off over the blue; while the small tentacles, or digitella, that spring from this margin are pure white. The larger tongue-shaped vesicles on the arms and oral disc have a greenish yellow color with a bluish green longitudinal stripe. The smaller vesicles on the arms are colored in a similar way and are inconspicuous, but the cluster of very small vesicles that occupy the greater part of the oral disc has a very different appearance, being lightly tinted by fine reddish brown pigment spots.

The two specimens that I have called variety *C*, are somewhat differently colored. The markings are yellowish white. The circular white band is indistinct. The rhopalial bands are interrupted at the margin of the concavity of the exumbrella, and stop short about half a centimeter from the rhopalial hood. At the margin of the umbrella there is a white spot on each rhopalial lobe and a strap-shaped spot on each velar lobe. The centre of the umbrella is whitish and opaque, so that the stomach does not show through. The oral arms are translucent, milky white tinged with brown, and without distinct white markings, except on the dorsal side of the principal branches. The large oral vesicles are yellow and greenish yellow, with a brown centre.

Size. — The diameter of the largest specimen found is 24 cm., while the smallest specimen that contained eggs measured 6.5 cm. The average diameter of twenty-three adult specimens was 13.7 cm. The relative sizes of the parts are exhibited in the following tables. Table 1 shows what may be regarded as the normal proportion for the species, though, to be sure, some of the measurements were made only on Port Royal specimens. Some of the dimensions were measured on a smaller number of specimens, and for these the average diameter of the umbrella of the specimens on which these measurements were made is given separately to show the correct proportions. Table 2 furnishes a means of comparing the proportions in the three varieties.

TABLE 1. DIMENSIONS OF SPECIMENS FROM BOTH SALT POND AND PORT ROYAL (VARIETIES *A* AND *B*.)

	Number of specimens measured	Average dimensions in centimeters	Average dimensions in thousandths of average diameter	Maximum (In thousandths of diameter unless otherwise noted.)	Minimum	Remarks
Diameter of umbrella	21	14.33	1000	24 cm.	9 cm.	Salt Pond and Port Royal specimens taken together.
Length of arms measured from centre of oral disc	21	11.21	782	888	642	
Length of central vesicle	21	2.71	189	287	103	
Length of primary vesicle	21	1.82	126	190	71	
Diameter of umbrella	10	15.79	1000	24 cm.	12 cm.	Port Royal only.
Length of radial vesicle	10	3.01	190	250	117	
Diameter of umbrella	11	13.62	1000	16.3 cm.	6.3 cm.	Salt Pond and Port Royal.
Diameter of stomach	11	4.22	311	333	292	
Diameter of umbrella	3	18.66	1000	24 cm.	15 cm.	Port Royal.
Thickness of umbrella	3	1.33	71	73	70	
Total depth	3	3.59	191	212	173	
Diameter of umbrella	2	20.50	1000	24 cm.	17 cm.	Port Royal.
Diameter of oral disc	2	8.00	390	441	354	

TABLE 2. AVERAGE DIMENSIONS OF THE THREE VARIETIES, GIVEN IN THOUSANDTHS OF THE AVERAGE DIAMETER OF THE UMBRELLA.

	Variety *A* Salt Pond	Variety *B* Port Royal	Variety *C* Port Royal
Length of arms	850	715	818
Length of central vesicle	157	217	—
Radial vesicle	—	190	163
Primary vesicle	112	138	167
Diameter of stomach	298	311	322
Thickness of umbrella	—	71	80
Total depth	—	191	213
Radial diameter of oral disc	—	390	394
Interradial diameter of oral disc	—	390	470

Locality. — Great Salt Pond, and mangrove swamps ("The Lakes") in the rear of Port Royal, Jamaica.— BIGELOW.

(?) Moat outside Fort Jefferson on Garden Key, Tortugas Islands, and Mangrove Keys, near Key West, Florida. — FEWKES.

ANATOMY.

Form of the Body. — To one who is familiar with the cyaneas, aurelias, and the like, of our northern coast, the shape of this medusa appears very strange. The aboral, or exumbrellar surface (Fig. 35), instead of being convex in *Cassiopea xamachana*, as it is in the great majority of medusae, is concave when the animal is at rest, except for a slight convexity over the stomach, and except in the region of the thinner marginal part of the umbrella, where also it is convex. The surface of the subumbrella, on the other hand, is convex, except in this same thinner marginal area, where it is in turn concave. The umbrella thickens very gradually from its margin to the centre, and the elevations and depressions of its surface have very gentle slopes, so that its general shape is much nearer that of a flat disc than the dome-like form of most medusae (Fig. 35).

A circular column arises from the centre of the oral surface of the umbrella. It is broad, but very short; and a few millimeters from the umbrella it loses its circular outline, owing to eight stout arms that spring from it at regular intervals (Fig. 34). These are smooth and rounded, except along a line on the oral side, where they bear the fringe of oral appendages, and they are long and much branched. This column is the *oral disc*, and its arms the *oral arms*.

The Structure of the Mesogloea. — By far the greater part of the mass of the oral arms and disc, as well as the umbrella, is composed of a firm, elastic, gelatinous substance, the *mesogloea*, and it is to this that the shape of the body is due.

The description given by Keller (**'83**), of the structure of the mesogloea in *C. polypoides* would apply almost equally well to our species. The mesogloea consists of a hyaline matrix, in which are imbedded certain fibres and three kinds of cellular elements. Most of the fibres appear to be analogous to connective tissue fibres, and take a general course through the mesogloea at right angles to the surface. Others seem to be protoplasmic. At any rate, they may be observed to proceed from the star-shaped cells that are scattered throughout the jelly.

The cellular elements are: the star-shaped cells, just mentioned; vesicular bodies, found in certain restricted localities; and the green cells, which, as it will be shown later, are symbiotic plants.

The star-shaped cells remind one of osteoblasts, and are probably analogous to them, in that they are concerned in the formation of the jelly. Hamann (**'81**) has called them *colloblasts*. They are small, often somewhat elongated, and have a well-marked nucleus.

The vesicular bodies give rise to the white markings that were mentioned in the description of the species. These vesicles are much larger than the colloblasts. Each one seems to be made up of a wall of exceedingly minute refractile granules, surrounding a clear space. That this body is a cell, however, is shown by the presence of a nucleus pressed closely against one side.

The green cells, or *zoanthelae*, are widely distributed throughout the mesogloea, but are most abundant in the umbrella. They are not infrequently found imbedded in the endodermal epithelium. The living cells have a greenish brown color, which they impart to the animal as a whole. They are of considerable size, are globular, without projections of any kind, and are generally to be found in clusters of two or more (*za*, Figs. 52, 56, and 63). Each one contains a nucleus and numerous granular bodies, and apparently is surrounded by a cell wall; but the latter is hard to distinguish from the edge of the adjacent matrix.

Keller thought that similar bodies in *C. polypoides* could not be algae, because he failed to find any evidence of a cellulose cell wall. He regarded them, therefore, as essential elements of the "mesoderm."

In those of my specimens, however, which have been killed in Erlicki's fluid and stained with borax carmine, the nucleus of these cells is found to be red, while the granular contents of the cell are bright green, and there are often one or two green bodies present that are as large or larger than the nucleus. They have all the appearance of chlorophyl bodies, and it is well known that the chlorophyl of some algae is not readily removed by alcohol. Moreover, in teased preparations treated with iodine solution these cells are found to be filled with granules that quickly turn deep blue, — evidently starch. The test for cellulose with iodine followed by sulphuric acid, gave, however, unsatisfactory results. The outline of the cell would become distinctly darker, but not recognizably blue. In the same way with chloriodide of zinc, a very marked reaction for starch was obtained, the granules becoming almost black; but so long as the object was viewed by direct transmitted light, no reaction for cellulose could be detected with certainty. On the other hand, when the light was thrown upon the object obliquely by means of a condenser with a central diaphragm, the effect was quite different. The starch granules became a deep ultramarine, and the parts of the cell not occupied by the starch appeared distinctly violet, showing without doubt the presence of cellulose.

Both starch and cellulose, as well as some form of chlorophyl, having been demonstrated in them, there can be no further question that the green cells in Cassiopea are symbiotic algae.

The Oral Arms and their Branches. — The eight oral arms (Fig. 34) arise from the central oral disc at about equal intervals; and when an arm is extended, the distance from the centre of the oral disc to the tip of the arm about equals three quarters of the diameter of the umbrella. But the arms are very contractile, and may be shortened to half this length. The arms are slender and graceful in shape, the mesogloea tapering very gradually to the tips of the finest branches. The branches are arranged alternately. The largest one, which is the first formed, is at a point about two thirds the length of the arm from its base. From this point the branches decrease in size gradually toward the base of the arm, and more rapidly toward the apex. The general outline of the arm, therefore, including its branches, is roughly spatulate.

The Oral Funnels and Brachial Appendages. — Just below the surface of the oral side of each arm there is a longitudinal tube, the *brachial canal,* that ramifies to each branch, and finally opens to the exterior by funnel-shaped *oscula* (*os.*, Fig. 34) at the tips of the numerous ultimate branches, and at many places along the course of the tube. The margins of these oscula, or oral funnels, are provided with short tentacle-like projections, the *digitella.* These are covered by an epithelium containing nettle cells, and each has a gelatinous axis in which there are transverse plates of greater density than the rest of the jelly, and these give the structure the cellular appearance first described by Hamann (**'81**). The epithelium lining the tubes and funnels is ciliated.

There open also into the brachial canals the lumina of the oral vesicles (*v.*, Fig. 34). These structures, as already stated in the diagnosis, have their points of attachment in the axils of the branches. All except the smallest are flattened laterally. The smaller ones are oval in outline, the larger ones linear. At one side near the apex there is a cluster of short processes that Hamann has homologized with digitella.

The Oral Disc. — Although the eight oral arms seem to be placed at equal distances and to be alike, they are morphologically in pairs, each pair being homologous to one of the four lips of a semostomous medusa, — an aurelia, for example. The line that separates two members of a pair is therefore, according to Haeckel's nomenclature a perradius. The brachial canals from each pair of arms, on entering the oral disc, converge and unite into a single radial tube that is continued to the centre of the disc, where it unites with the other three. In this way the course of the tubes on the oral disc forms a pattern that resembles a Maltese cross. The larger *central vesicle* is attached at the centre of the cross. In a living specimen 11 cm. in diameter this measured 3 cm. in length. There are four other vesicles that most nearly approach the central one in size, and these arise from the radial canals near the junction of the brachial canals, and I have called them, therefore, the *radial vesicles.* In full-grown individuals there are eight more vesicles upon the oral disc, a little smaller than the last, one on each brachial canal distal to the junction. It is only near the periphery of the disc that the canals are provided with oral funnels. For most of their course on the disc the canals give rise to the very small vesicles, finely speckled with a reddish brown pigment, that already have been mentioned. These have nettle batteries at their tips, and are so numerous as to cover completely the greater part of the disc and to hide the course of the canals. This mass of small vesicles, however, is not acquired until late. Specimens as much as 6 cm. in diameter will be found to be without them. In such specimens we have the five largest vesicles, and a number of oral funnels are scattered along the canals, just as they are upon the arms. This replacement of the oscula on the oral disc by small vesicles has been observed to occur also on adult females of *Polyclonia frondosa*, but not in the males (Bigelow, '93). It is not improbable therefore that a similar difference between the sexes may be discovered in our species of Cassiopea.

The Subgenital Cavities and the Digestive Tract. — At each of the four points of junction of the brachial canals there is a slit-like passage, oesophageal canal, dipping vertically into the mesogloea of the disc, and opening into the stomach. The latter is a lens-shaped cavity, with a gently arched roof. Its floor consists chiefly of four lozenge-shaped areas, where the body wall is very thin and plaited in radial folds (Fig. 34). These thin parts of the body wall form the roofs of the subgenital cavities, which open to the exterior, each by an elliptical orifice, *osteum*, (x, Fig. 34) in the side of the oral disc near the subumbrella and in the angle between two pairs of arms (interradial). The gonad appears as a band which crosses this membrane tangentially at its greatest width. Just central to each gonad there is a multiple series of very many small gastric filaments forming a narrow band parallel to the ovary. These are ciliated, and provided with nettle and gland cells. The portion of the floor of the stomach not made up of these lozenge-shaped membranes is bounded by the firm mesogloea of the oral disc. This area has the shape of a Maltese cross, and it is in the arms of this cross, between the subgenital cavities, that the passages from the oral canals open into the stomach.

Near its periphery the floor of the stomach is marked by radial grooves. These are continued, each into one of the radial canals that extend outward from the edge of the circular stomach to the marginal region of the umbrella. There are regularly thirty-two of these, sixteen in the radii of the rhopalia, and sixteen interrhopalial. When the number of rhopalia is increased, the number of radial canals may or may not increase in proportion. There are often thirty-four or thirty-six of them. The canals in the radii of the rhopalia are larger and more nearly straight than the interrhopalial ones, and all are connected by a fine network of anastomosing branches, among which no distinct circular canal can be recognized. The meshes in the network of canals are connected by a plate of endodermal cells, the *endodermal lamella*. This lamella is also in contact with the subumbrellar ectoderm along a line encircling the umbrella a short distance from its margin, so that there is a complete sheet of endoderm separating the subumbrellar from the exumbrellar mesogloea.

Musculature. — The exumbrella is devoid of muscles, but on the opposite side there is a continuous sheet of muscle fibres, which is spread over the subumbrella, except a narrow zone at its margin, and is continued over the oral arms to their finest ramifications, and also into the subgenital cavities.

Most of the fibres on the subumbrella do not take an evenly circular course, but are undulating. They form in this way a series of double "arcades" like those found by Haeckel in other species of Cassiopea. There is one of these double arcades for each interrhopalial space. The surface of the mesogloea in this region is grooved. The sheet of muscle fibres lies directly upon it, and is therefore corrugated, the grooves being parallel with the fibres.

The muscular layer upon the oral arms is smooth, and its fibres take a longitudinal course, extending to the digitella and oral vesicles.

In the subgenital cavities the arrangement of the muscle fibres could not be made out; but their presence was revealed by the squirming movements of the thin membrane that separates the subgenital cavity and bears the gonads and gastric filaments.

Structure of the Marginal Sense Organs. — Each rhopalium has a pigment spot on the aboral side near the extremity, and each one lies in a deep sensory niche. The dorsal sensory groove, common in the Pelagidae, Aurelia, etc., is entirely lacking; although Keller found in *C. polypoides* a slightly depressed thickening of the ectoderm that corresponds to it. The sensory niche and rhopalium are, with the exception of the pigment spot, similar in all essential particulars to those found in Pelagia. The rhopalium is the only organ in the sensory niche (Fig. 56). It is a hollow, finger-like projection attached by its base to a low ridge that runs along the roof to the central wall of the niche. This ridge is penetrated longitudinally by the continuation of a radial canal from the stomach, and the lumen of the rhopalium opens into the distal end of this canal. In the distal half of the rhopalium the lumen is nearly obliterated by the increase in thickness of its endodermal lining. Here the endoderm, instead of being a columnar epithelium as elsewhere, is a mass of parenchyma-like cells, each of which contains a large calcareous concretion, a so-called otolith. A thin, supporting membrane separates the endoderm from the ectoderm. At the distal extremity of the rhopalium the ectoderm is a thin, cuboidal epithelium, while over the rest of the surface it is a thick, sensory epithelium resting on a thick network of fine nerve fibres. This, in turn, rests on the supporting membrane. I have observed no ganglion cells in this layer of nerve fibres, which is continued under the epithelium of the rhopalial ridge to the central wall of the niche, where it becomes imperceptible. There are no thickened bands of these fibres running to ciliated pockets, such as are found in Dactylometra (Bigelow, '90), and the fibres probably spread out finally into a thin network underlying the general epithelium of the subumbrella.

The one feature in which this rhopalium differs from what is found in Pelagia is the presence of the pigment spot, already mentioned, lying on the aboral side of the rhopalium immediately above the centre of the mass of concretions. This area is probably sensitive to light, but it only differs from the rest of the sensory epithelium in that here the superficial cells are deeply colored by a yellowish brown pigment. A more careful examination would undoubtedly show the histology of this structure to be similar to what Schewakoff ('89) has found in Aurelia.

HABITS.

The species of Cassiopea and the closely related genus Polyclonia find their habitat usually in quiet lagoons among the mangroves along the shores of the tropical seas. The mode of life of several species has been described by Brandt ('38) on the authority of Mertens, L. Agassiz ('62), Gray ('69), A. Agassiz ('81), Archer ('81), Fewkes ('82), Guppy ('82), and Agassiz and Mayer ('99). *Cassiopea xamachana* is no exception to the rule either in its habitat or its sedentary mode of life.

When the young medusa is set free from the strobila it is an active swimmer. It gradually becomes less active as the mouth parts acquire their adult structure, and by the time the animal has reached a diameter of two centimeters it has definitely taken up its abode upon the bottom. It lies there, as described in the Introduction, with the oral appendages upward, and seldom changes its position unless disturbed. The concavity of the exumbrella is an important aid in maintaining this posture against the action of waves and currents. The gelatinous tissue is firm and elastic, and causes the umbrella to assume its normal shape when the subumbrellar muscles are relaxed. The slight suction thus produced when the medusa comes to rest on a flat surface gives it such a hold that a certain amount of force is required to remove it.

Usually, however, the water in the lagoons is very quiet, and there is more danger from its stagnation than from its motion. A Cassiopea is enabled to avert this danger by the slight swimming movements of the thinner marginal part of the umbrella. By means of these rhythmic contractions the water is drawn in on all sides, and then is driven upward and away. A healthy specimen lying undisturbed on the bottom of an aquarium was observed during seven minutes to make on the average 19.7 contractions of the umbrella per minute. In this way the animal is enabled to draw to itself a fresh supply of oxygen and of its minute food material.

The oral arms and their branches are usually spread out so as to cover the subumbrella completely, but they are almost always in motion, bending to one side or the other, and they may be flexed aborally until the tips come within the umbrellar margin, or extended until they reach far beyond. Besides these general movements, the various appendages of the oral arms have movements of their own. Muscular contractions may be observed also in the thin membrane that separates the stomach from the subgenital cavities, and they probably serve to renew the water that bathes the gonads.

When the oral disc has been severed from the umbrella, both parts may remain alive for several days, and both retain their powers of spontaneous movement. The first effect of the operation is often to throw all of the parts into a strong tetanus, but shortly afterwards the pulsations of the umbrella may be renewed at a rate considerably more rapid than normal, — 32 to 34 per minute in one case. When the medusae have been for some time under unfavorable conditions, it frequently happens that the part of the body-wall surrounding the periphery of the stomach is ruptured, and thus the mouth parts as a whole become separated automatically from the umbrella.[1]

While at Bimini, Bahamas, in 1892, I observed that the food of *Polyclonia frondosa* consists chiefly of copepods and other small crustacea, and that these are caught by the combined action of the oral vesicles and the oscula ('**93**, p. 106). If a copepod strikes a vesicle, the vesicle bends quickly so as to cover the mouth of the adjoining osculum, and the copepod is thus enclosed in a trap. Artificial stimulation would cause the same reaction.

Experiments on *Cassiopea xamachana* made to determine whether or not this species obtains its food in the same way gave negative results. Stimulation of an oral vesicle causes only a slight bending on the side stimulated. Although these vesicles are provided with batteries of nettle cells near the tip, I was unable to see that they played any part in the taking of food. It may be that they are protective, but the sting is very feeble.

Examinations of the contents of the stomach were almost equally unsatisfactory. The contents of twenty-two stomachs were examined, and of these fourteen contained only a clear, very viscous fluid and, in some cases, a few apparently ripe eggs, more or less distorted, some small, colorless cells, probably sloughed off from the endodermal epithelium, and green cells identical with the "zoanthelae" found in the mesogloea. One or more copepods and other crustacea were found in five specimens. In one of these one small amphipod was found, and in another the cornea of an unknown crustacean.

---

[1] While this paper is passing through the press a paper has appeared by E. W. Berger (**1900**), in which he gives the results of experiments made by F. S. Conant upon Polyclonia and Cassiopea to test the effect of removing the rhopalia.

Diatoms and other algae, exclusive of the above-mentioned zoanthelae, were found in four cases out of the twenty-two. Almost always the first impression on opening a stomach was that it was empty; and it was only by careful examination that the contents of the stomach could be discovered. In two cases, however, a considerable amount of material was found in the stomach. In one of these the stomach contained, besides the usual eggs, zoanthelae, debris, etc., the remains of many copepods, some nematods, a zoea, and some diatoms. In the other one there was found a compact greenish mass, about one centimeter in diameter, composed of granular debris and diatoms of various species, together with some desmids, Oscillaria, foraminifera, infusoria, Vorticella, and some fine filaments with spirally arranged contents.

This species exhibits the power of regeneration of lost parts to a marked extent. Specimens were frequently met with in which branches of the oral arms, or even portions of the margin of the umbrella, had evidently been formed recently to replace parts that had been destroyed. Moreover, branches of the oral arms that had been cut off were observed to regenerate oscula and vesicles at the central end.

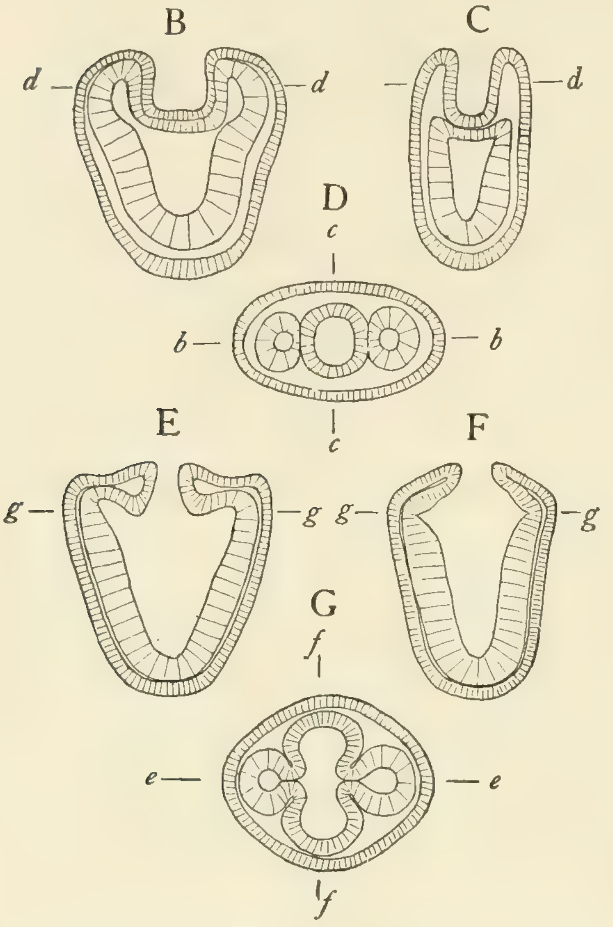
ONTOGENY.

Historical Review. — Numerous studies upon the reproduction of various animals by budding have shown that the formation of organs in the bud may take an entirely different course from the development of homologous organs in the sexually produced embryo. As the observations to be described in the sequel were made entirely upon larvae that were observed, or supposed, to be asexually produced, they cannot settle any of the disputed points in regard to the development of sexually produced larvae. Nevertheless it will be of interest to compare the sexual with the asexual mode of ontogeny, especially as the development of a scyphistoma from a bud has never before been fully described.

The development of scyphomedusae from the egg has been studied in comparatively few forms. Several species of Aurelia have been studied by Sars, Haeckel, Schneider, Claus, Goette, Frank Smith, and Hyde. Two species of Cyanea have been studied by McMurrich and Hyde. A species of Chrysaora has been studied by Claus; and Kowalewsky, Metschnikoff, Krohn, and Goette have traced the very interesting abbreviated development of *Pelagia noctiluca.* The nearest ally of our species that has been studied with any degree of completeness is the Mediterranean rhyzostome *Cotylorhiza tuberculata,* which has been the subject of investigation by Claus and Goette.

From the description of the process of budding given in the next section, it will be noted that the larvae produced by budding are set free in a form resembling planulae, and it is the planula stage in sexual reproduction which is the earliest that can be compared with any stage to be described in this paper.

All agree that the planula of the Scyphomedusae is a more or less oval, ciliated larva, somewhat flattened on one side. It consists of two layers of cells surrounding a cavity which is completely shut off from the exterior. The first step toward the development of the scyphistoma is an invagination of the ectoderm at the posterior pole of the planula. According to Goette and Miss Hyde, the endoderm is invaginated at the same time in such a way that two endodermal pouches remain in the plane of the long diameter,—"Hauptebene," Goette,— (Fig. B, and *b–b* Fig. D), one on each side of the invagination, while the endoderm is pushed entirely away from the oral pole in the plane of the short diameter (Fig. C, and *c–c* Fig. D). The ectodermal invagination is the oesophagus (Schlund), its external opening is the mouth, and the endodermal evaginations are the first pair of gastric pouches. Soon an opening is formed (Schlundpforte) between the base of the oesophagus and the central stomach, and at the edge of the opening the ectoderm fuses with the endoderm. Then the second pair of gastric pouches is formed. According to Goette these are produced in Cotylorhiza and Pelagia entirely from the ectoderm of the lower part of the oesophagus (Fig. F). According to his view the lower edges of these evaginations coincide with the margin of the gastro-oesophageal opening (Schlundpforte), and are therefore at the level of the upper edges of the first pair of pouches. As these pouches extend out-



Figs. B–G. Two stages in the development of the mouth and gastric pouches in a sexually produced scyphistoma, according to Goette. Figs. B to D are sections in the three dimensions of space of a larva in which the oesophagus is invaginated and the first pair of gastric pouches are formed. Figs. E to G are similar sections of a larva in which the opening from the oesophagus into the stomach (Schlundpforte) has been established and the second pair of gastric pouches are in the process of formation. *b*, *c*, *d*, etc., indicate the plane of Figs. B, C, D, etc.

ward the ectoderm is pushed out until the principal radii) *e–e* and *f–f*, Fig. G) gradually become equal. This results in the formation of the flattened peristomal disc (Figs. E and F). At the same time the wall separating the oesophagus from the first pair of gastric pouches (Taschenvorhang) is split upward until the openings into the two pairs of pouches are upon the same level, and the "Taschenvorhang" is reduced to a low ridge, while the oesophagus is very much shortened. Portions of the original lining of the lower part of the oesophagus persist as the covering of the inner edges of the septa which separate the four gastric pouches. The larva is now in what Goette calls the scyphula stage. He regards this stage as of great phylogenetic importance, showing clearly, he thinks, a close genetic connection between the Scyphomedusae and the Anthozoa; so that these groups should be placed in a single class, Scyphozoa, to distinguish them, on the one hand, from the Hydrozoa, including the hydroids, hydromedusae, and, on the other, from the Siphonophorae.

This view, which is confirmed by Miss Hyde, is antagonized by Claus, and has given rise to a prolonged controversy. The parties to this dispute are practically in accord in regard to the facts of observation, as represented by the figures in their latest contributions. It is in the interpretation of these facts that they differ mainly. Claus (**'90**) admits that there is an ectodermal invagination previous to the formation of the mouth, and that the lining of the proboscis is ectodermal. He maintains, however, that the condition represented in Figs. B, C, and D, is due to a severe contraction of the animal, and is without morphological significance. He denies that there is any oesophagus, "Taschenvorhang," or "Schlundpforte," in the sense that Goette uses these terms; and with these he rejects the idea of a close affinity between the Anthozoa and scyphomedusae, with the correspondingly sharp distinction between the latter and the hydromedusae. He admits, however, that a distinction of importance between scyphistoma and hydropolyp is to be found in the possession by the former of an ectodermal lining of the proboscis, and in the presence of gastric pouches and septa.

Goette's position has been strengthened considerably by his latest contribution on this subject (**'93**), and his conclusions are confirmed in nearly every particular by Miss Hyde. Goette's figures appear to be camera drawings of serial sections, and are a great improvement over the rather diagrammatic illustrations in his earlier papers. They are not entirely convincing, however, for the ectoderm and the endoderm grade into each other so that it is impossible to determine the exact boundary; and the material is so subject to distortion during the preservation that it is often difficult to determine whether a given fold of the epithelium is of morphological value or is merely an artifact.

Miss Hyde fails to confirm the view that the whole of the second pair of gastric pouches (and hence, according to Goette, five eighths of the peripheral digestive tract of the medusa) is of ectodermal origin. On page 550 of her paper she speaks of only the roof, i. e., the lining of the oral side, of these pouches as formed from oesophageal ectoderm, and her sections bear out this view.

The foregoing brief summary of the present state of knowledge regarding the early stages in the development of the sexually produced scyphistoma will serve as an introduction to what is to follow. Mention of the work of others upon the later stages will be made when we come to the corresponding periods in the development of *Cassiopea xamachana.*

The Formation of the Bud. — In 1841 Sars described the budding of scyphistomas that were supposed to belong to a species of either Aurelia or Cyanea. The buds, according to this account, may grow out directly from the main part of the body of the larva, or they may be produced on stolons extending outward from the foot. In either case, several buds may be formed, apparently in various positions on the scyphistoma at one time. The figures show the buds attached to the parent and provided with a well-developed crown of tentacles at the distal end. Agassiz (**'60**) found a similar process of budding to occur occasionally in Aurelia. Goette (**'87**) has confirmed these observations, and has found that the larvae of *Cotylorhiza tuberculata* also produce buds.

In Cotylorhiza the bud is formed as an outgrowth from the body of the scyphistoma; and as it grows it gradually approaches the shape of its parent, but its relative position is just the reverse of what Sars found; for the distal end forms the stem, and the proximal end begins to flatten out into a circumoral disc. In this condition the bud is set free, and swims about, rotating on its long axis, with its distal end forward. The mouth is formed at the point where the constriction finally separates the bud from its parent, and the larva fixes itself by the opposite end.

Claus (**'92**) has found that the scyphistomas of Cotylorhiza not only produce buds, but that they produce them in large numbers. Scyphistomas reared from eggs that had been laid in September, 1890, were kept alive in the aquaria at Trieste and Vienna throughout the following winter and spring. No change was observed after the larvae had reached the sixteen-tentacle stage, until the following July, when budding occurred. The process was not restricted to a few well-nourished individuals, but seemed to be a general and repeated phenomenon, and it resulted in a large increase in the number of larvae. Claus's brief description of the formation and fate of the bud, accompanied by three figures, corresponds perfectly with what I have to describe in the following pages. The strobilization, he says, took place in August, and was monodiscous.

Another case of rapid multiplication of scyphistomas by budding is described by Lacaze-Duthiers (**'93**). A colony of these larvae, of unknown origin, was discovered in an aquarium at Banyuls in 1892. No strobila or ephyra was observed up to October, 1893, but in the meantime the number of scyphistomas had increased enormously. The buds appeared as elevations on the side of large individuals. The base of this elevation became elongated into a filamentous stolon carrying the bud at its tip. The bud fixed itself to the glass, gradually developed tentacles, and finally became independent by the disappearance of the stolon.

In *Cassiopea xamachana* the process of budding is an important, if not the chief, factor in the perpetuation of the species. On looking over collections of scyphistomas taken from the Great Salt Pond during May, June, and July, a considerable number was found with buds attached in various stages of development (Figs. 1, 2, and 26), and budding continued in the aquaria.

There is no stolon. The first visible rudiment of the bud is a slight swelling on one side of the calyx just above where it tapers into the stem. It involves all three layers of the body wall (Fig. 36). At an early stage in the growth of the bud the four septal muscles may be found as four slender cords of cells embedded in the mesogloea and apparently growing out from a thickened area of the ectoderm at the apex of the bud (*sm*, Figs. 38 and 39). This appearance seems to indicate that the septal muscles of the bud are formed, as in sexually produced scyphistomas, by an ingrowth of the ectoderm.

Careful study of serial sections through young buds shows, however, that the septal muscles of the bud are connected with septal muscles of the parent. In Fig. 37 the course of the septal muscles is reconstructed from a series of longitudinal sections. The muscle sm_1 passes around the base of the bud on the side away from the observer and gives rise to two branches, sm'_1 and sm'_3. These extend toward the apex of the bud, and each one divides dichotymously. Muscle sm_4 gives off a branch which fuses with sm_1, at the base of the bud. Sm_2 produces three branches which unite into a single branch. This branch extends into the base of the bud, but it was impossible to trace it further. It may be connected, perhaps, with the muscle sm'_2, which was traced for a short distance from the apex of the bud.

On account of the presence of the muscles, it is possible to study the relation of the plan of symmetry of even young buds with the symmetry of the parent. A series of sections made at right angles to the long axis of the bud shows that the vertical perradii of the bud lie in the plane of one of the perradii of the parent. But in transverse sections it is impossible to trace the muscles of the bud, except for short distances, owing to their extreme fineness.[1]

However, the study of longitudinal sections makes it reasonably certain that the septal muscles of the bud are derived from outgrowths of one or both of the septal muscles of the parent which lie in the interradii adjoining the perradial area of bud formation. If this be true, then every part of the young bud is formed from the corresponding part of the parent, viz., — ectoderm from ectoderm, mesogloea from mesogloea, endoderm from endoderm, muscles from muscles, and digestive tract from digestive tract. There is no indication of any method of budding of the kind described by Lang ('**92**).

---

[1] The position of the bud is always perradial, although in some preparations it appears to be interradial, owing to the obliquity of the sections, as in Fig. 36.

In the young bud the mesogloea is very thin, so that the ectoderm and endoderm are very nearly in contact. The evagination gradually increases in size, becoming first hemispherical and then more elongated. At the same time a constriction appears close to the body of the scyphistoma, which deepens until the bud becomes a spindle-shaped body attached to its parent by a short and narrow stem consisting of a film of mesogloea covered with ectoderm, the digestive cavity of the bud being entirely closed (Fig. 1).

Scyphistomas are never found with more than two buds attached. When two buds are present they are always of different ages, and the elder is always attached to the apex of the younger (Fig. 2).

The Planula-like Larva. — When finally constricted off, the bud is a simple, spindle-shaped, hollow body, without trace of mouth or tentacles. It is like a planula in form and habits. The whole surface is covered with cilia, and it swims about, rotating from right to left upon its long axis. In swimming, the distal end is directed forward. While swimming, the larva is constantly changing its shape, assuming in a few minutes various forms from an elongated spindle to a short heart-shape (Fig. 3, *A*, *B* and *C*). It swims near the bottom, hiding under any object that it may find there. When it strikes an obstacle, it may rest there quietly, or it may rotate slowly upon its long axis. In all its movements it reminds one very strongly of Agassiz's description of the planulae of Aurelia.

The larva is white, speckled with a few greenish brown spots. It is rather opaque, but much of the structure may be seen in a living specimen. A longitudinal section shows that the ectoderm consists of a deep layer of very narrow and closely-packed columnar cells (Fig. 39). The mesogloea contains a few green cells (producing the greenish brown spots), and some widely scattered colloblasts. The layer is thickest at the equator, diminishing gradually to a very thin layer at both ends. The four septal muscles (*sm*) are seen clearly at the distal end of the larva, embedded in the mesogloea and united with the ectoderm near the apex (Fig. 38). In one specimen, not yet detached from the parent, it was possible to trace one of the muscles all the way from the proximal to the distal end. The muscle fibres are already differentiated and line the tube of mesogloea, while the nuclei occupy a central position.

The endoderm is a columnar epithelium, rather thin, with the cells closely packed together and coarsely granular at the proximal or posterior end of the larva. Toward the equator the cells become higher; and at the distal, or anterior, end they are large and clear. The character of the endoderm makes it possible to identify the anterior end of the swimming larva with the distal end of the bud.

The Formation of the Mouth. — The first change to be seen in the swimming larva is the formation of the mouth, which occurs two or three days after the larva has been set free. When writing my preliminary paper ('92 a), I was in doubt as to the relation between the poles of the bud and those of the larva. The better and more abundant material obtained during the second visit to Jamaica proved conclusively that the proximal end of the bud forms the oral end of the larva, just as it does in Cotylorhiza, according to Goette. The identification is made easy by the polar differentiation of the endoderm described in the previous section.

When first seen the mouth looks like a minute pin-hole in the posterior end of the larva (*m*, Fig. 4 *B*). In longitudinal sections at this stage the first indication of the formation of the mouth is the disappearance of the mesogloea from a small area at the posterior end, so that there is no longer a distinct boundary there between the ectoderm and endoderm (*m*, Fig. 40). At the same time a small dent appears in the outer surface. This deepens until it forms a minute tube connecting the endodermal cavity with the exterior (Fig. 41). The mouth thus formed gradually widens and becomes slightly funnel-shaped.

Further stages in the development of the mouth are represented in Figs. 5, 6, 7. In In Fig. 6 there is a distinct circular groove which outlines the base of the proboscis and separates it from a rudimentary peristome. In Fig. 7 the peristome is well developed, and the mouth is widely open.

There is no invagination of the ectoderm connected with the formation of the mouth, and there is no oesophagus, "Schlundpforte" or "Taschenvorhang." So, if Goette's account of the formation of the mouth in the sexually produced scyphistomas be accepted, we have here a case where an agamogenetic differs to a marked degree from the gamogenetic course of development.

The Scyphistoma. — With the elongation of the forward end, the formation of tentacles, and the development of four gastric pouches, the free-swimming larva becomes a typical scyphistoma.

By the end of the third or fourth day after the bud has been set free, the forward end of the larva has elongated to form a stem equal in length to the rest of the body (Figs. 7, 8, 9, and 11). The end of the stem becomes expanded, generally flattened, and the epithelium covering it becomes deeper than the rest (Fig. 42). This epithelium produces a secretion which serves to fasten the larva to some solid object. Fixation usually takes place during the fourth or fifth day, but the time varies greatly.

Development of the Tentacles. — During the third day the peristome appears as a minute ridge surrounding the posterior end of the larva, a short distance from the mouth. The first series of tentacles arises during the following twenty-four hours as four perradial angles in the margin of the peristome (Fig. 8). Four interradial tentacles appear almost simultaneously with these, or sometimes considerably later (Figs. 9, 10, 11, and 12). The elongation of the tentacles takes place rapidly, so that at about the end of the sixth day the peristome is surmounted by a crown of eight tentacles, which equal the proboscis in length.

With the broadening of the peristome the differentiation of the body of the scyphistoma into stem and calyx becomes apparent externally (Figs. 13 and 14). When the eight perradial and interradial tentacles have become long enough to reach some distance beyond the mouth, eight adradial tentacles appear in the angles between them. In Fig. 14 the adradial tentacles are distinctly developed, and two of the tentacles of the first series are bifurcated near the base. Figs. 15 and 16 represent the typical scyphistoma in the sixteen-tentacle stage. The tentacles are now long and graceful, and thickly dotted with batteries of nettle cells.

When fully developed, the scyphistoma is about one millimeter and a half in diameter; and it is provided typically with thirty-two tentacles.[1] But there is as much variation in the number of tentacles in the scyphistoma as there is in the number of sense organs and parameres in the adult. The number of tentacles is seldom less than thirty-two, often greater. The way in which this variation takes place is indicated in Figs. 21 and 14. All degrees of anomaly may be observed, from a bifurcated tentacle shown at x in Fig. 21, through the condition represented in Fig. 14, to two completely separated tentacles occupying the position of one typical one.

The tentacles of a well-developed scyphistoma, when fully expanded, exceed the length of the body several times. According to the position in which they are held, the tentacles may be divided into two series. Those of one series are held nearly erect, while those of the other series, consisting of the alternate tentacles, are bent backward until their tips nearly touch the ground upon which the animal rests. The action of the tentacles in capturing prey may be observed in a small aquarium, under the microscope. As soon as a tentacle comes into contact with a small floating body, such as a copepod, it is whipped quickly into the mouth, and at the same instant the side of the mouth toward the tentacle is opened more widely. On one occasion I saw two tentacles make captures at the same time, and the mouth expanded in both directions at once, showing a close co-ordination between the movements of the tentacles and of the mouth.

---

[1] Specimens have been found with twenty-four tentacles, but it is uncertain whether this is a regular stage in development between the sixteen- and thirty-two-tentacle stage, or a duplication of tentacles of the earlier stage.

Development of the Gastric Pouches. — While the final result is the same, the method of development of the gastric pouches differs entirely in our larva from the process as described by Goette. The free-swimming larva is somewhat flattened laterally (Fig. 4), and the long and short diameters are in the planes of the perradii. But there is no evidence that the gastric pouches in the long diameter are formed any earlier than those in the short diameter, and the ectoderm plays no part in their development. The formation of the gastric pouches is usually described as a process of evagination; but in this case, at least in the earliest stages, the delineation of the pouches seems to be due rather to the ingrowth of the septa.

These appear at the time of the formation of the first tentacles (Fig. 8) as four minute vertical folds of the endoderm (*sep*, Fig. 43), placed equidistantly in the angle formed by the peristomal fold (compare Fig. 42). The mesogloeal portion of the septum is at first very thin, and in the four-tentacle stage (Figs. 8 and 43) is no higher than the thickness of the endodermal layer of cells. The septal muscles do not penetrate the septa at this stage. While well-developed below, they can be traced upward only to within 35 or 41 μ[1] from the base of the septa.

In the eight-tentacle stage (Fig. 13) the septum is still very small, and the septal mesogloea near the margin of the peristome is very thin, hardly thicker than a cell wall. But at the central margin it has increased in thickness, and now the septal muscle may be traced from the stem upward through this thickened portion of the septal mesogloea to the peristomal ectoderm (*sm*, Figs. 44 and 47). It is impossible to determine whether the new portion of the septal muscles is formed by growth upward of the muscles already present in the stem, or whether it is the result of a proliferation of the peristomal ectoderm which may grow downward and fuse with the older portion of the septal muscles.

The four septa are now complete, and divide the digestive cavity into a large central stomach, extending into the stem, and four shallow marginal gastric pouches. The gastric pouches expand with the growth of the peristomal disc, so that the ectoderm and endoderm remain in close contact at the margin; while the central edges of the septa retain their original relative position. Thus the gastric pouches and the septa become deeper as the larva increases in size. This is evident in the sixteen-tentacle stage (Figs. 15 and 45 to 49). It will be shown later that the relation of the interradial tentacles to the septa is variable. In this stage, however, the distal part of the septal mesogloea has begun to disappear, so that immediately under the interradial tentacles the endoderm of adjacent pouches is fused (Figs. 45, 46, and 47). In the fully developed scyphistoma this area of fusion is perforated, so that there is a communication between adjacent pouches, forming the "Ringsinus" of German authors. In the specimen with forty-two tentacles, from which the section represented in Fig. 51 was taken, this perforation was very small. Figs. 52 and 53 represent a little later stage, in which the opening has become much wider.

---

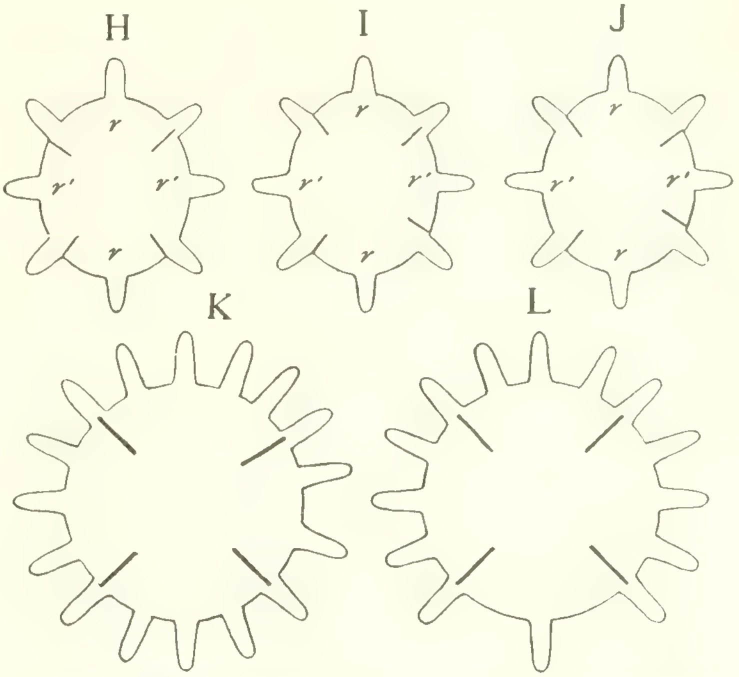
[1] 35 or 41 μ = about one seventh of the length of the larva.

Each septal muscle is a solid cord of cells, with a single layer of longitudinal muscle fibres in its periphery. In the peristome the fibres of the septal muscles spread out in a fan-shaped arrangement toward the margin.

Four slight interradial depressions in the peristome may be observed as early as the four-tentacle stage. They are deeper in the eight- and sixteen-tentacle stages, and the septal muscles may be seen to join the ectoderm at their bottoms. These depressions may be homologous with the septal funnels of the Stauromedusae, or they may be merely the result of the contracted condition of the larva. The question is of no importance, for there can be no doubt about the homology of the muscles; and whether they are solid or hollow is merely a matter of detail. In later stages (Figs. 51 and 52) sections seem to show that the peristomal depressions have deepened centrally so as to leave the insertion of the septal muscles high up on the peripheral side. But here, again, before any morphological conclusions can be drawn, account must be taken of the growth of the perradial angles of the proboscis and of the effect of the contraction of the septal and peristomal muscles.

Relation of Septa to Interradial Tentacles. — According to Goette, the interradial tentacles are always interseptal in origin. That is, two of these tentacles are produced as diverticulae from each of the second pair of gastric pouches (ectodermal), and their subsequent position in the planes of the septa is due to a secondary shifting. He finds in this important evidence in favor of his theory of the close affinity between the Scyphomedusae and the Anthozoa, for the tentacles of the latter are also invariably interseptal. Claus, on the other hand, finds that the interradial tentacles of Aurelia and Cotylorhiza are variable in origin. According to his observations (**'91** and **'92**), an interradial tentacle may be interseptal, that is, arise as a diverticulum of a single gastric pouch, the endoderm growing out and pushing the ectoderm before it; or it may arise in the plane of a septum by the union of two endodermal diverticulae, one from each of the adjacent pouches. He holds, therefore, that the origin of the tentacles cannot be used as evidence to uphold Goette's theory.

My observations on Cassiopea are in perfect accord with those of Claus. A number of series of transverse serial sections made from young scyphistomas in the eight- and sixteen-tentacle stages were studied carefully with the aid of camera sketches drawn on transparent paper. By this means the relations of the parts could be determined accurately; and the results are embodied in the series of diagrams, Figs. H to L. In the eight-tentacle stage, according to Goette, the gastric pouches in the long diameter, *r r*, should each give rise to a single tentacle, while the pouches in the short diameter, *r′ r′*, should each produce three. From a glance at Figs. H and J it will be seen that this is not the case in Cassiopea. To be sure, most of the tentacles at this stage are interseptal in position, but the interradial tentacles arise as often from pouches in the long diameter, *r r*, as from those in the short diameter, *r′ r′*; and in both Figs. H and I there is one interradial tentacle that is distinctly septal in position. The septa are still complete, so that there can hardly be any chance of a shifting of position. In the sixteen-tentacle stage, there is a tentacle in the plane of each septum (Figs. K and L); but here the perforation of the septa has commenced, and a shifting of relative position is possible. Even at this stage irregularities are common. For example, one of the septa in Fig. K is placed asymmetrically with relation to the tentacles, and two tentacles are wanting in Fig. L.



Figs. H-L. Diagrams illustrating the space relations between the septa and the tentacles, observed in five young scyphistomas of *Cassiopea xamachana.* r — radii of the long diameter, r′ — radii of the short diameter.

The Strobila,— Development of the Rhopalia.— When the scyphistoma has reached a diameter of about two millimeters, there appear the first characters that are distinctive of the strobila. The first noticeable change in this direction takes place at the bases of the tentacles of the more erect series. This change may be regarded either as the outgrowth of a conical lobe from the margin of the circumoral disc bearing the tentacle at its tip, or as a conical widening of the basal portion of the tentacle. The former view is probably the better. At about this time there appear in the tentacle, just beyond the apex of the cone from which it springs, a few glistening white bodies. These are the so-called otoliths, and mark the beginning of the formation of the rhopalium (Figs. 17 and 18). The tentacles containing these will be called the rhopalial tentacles.

These concretions, or otoliths, increase in number until they form a conspicuous mass, while the basal cone begins to broaden laterally. This is now distinctly noncontractile, and may be spoken of as a marginal lobe of the peristome (Figs. 19 and 20). In the specimen shown in Fig. 21 we see the first indication of strobilization. The upper, expanded part of the calyx is separated from a conical, lower portion by a slight groove. The marginal lobes have become semicircular in outline, and a slight elevation is noticeable on the aboral side of each rhopalial tentacle immediately external to the mass of concretions. The epithelium at this point is pigmented, and forms the first rudiment of the eye (*oc.* Fig. 22). Fig. 23 illustrates a more advanced stage, where the proximal part of the tentacle is beginning to take on its final shape, and is separated by a pronounced bend from the distal portion, which is still functional as a tentacle.

We come finally to a stage in which, while the long distal part of the tentacle retains its characteristic structure and remains completely functional, the short proximal part has become completely differentiated into a rhopalium. Fig. 54 is from a longitudinal section of such a tentacle. The rhopalial part has assumed nearly its final shape. The differentiation of its ectoderm into sensory epithelium, eye-spot, and layer of nerve fibres, is complete. It has a lumen that extends outward to the solid chorda-like endoderm of the distal part of the tentacle, and opens toward the centre into a gastric pocket. The endodermal lining of the lumen is a columnar epithelium, the more distal cells being deeper and containing the concretions. Compare Fig. 54 with Fig. 53, which, being interradial, was certainly destined to be a rhopalial tentacle.

The growth of the marginal lobes, which were semicircular at the stage of Fig. 21, has continued, and each lobe has now produced two secondary ones, one on each side of the rhopalial tentacle. These are connected by a slight ridge that crosses the base of the tentacle on its aboral side (*h.* Fig. 54). The secondary lobes are the rhopalial lobes of the margin of the umbrella (Flügellappen of German authors), and the connecting ridge is the hood (Deckplatte) that covers the rhopalium. These marginal structures may be seen in Fig. 24, and this brings us to another stage in the development of the rhopalium, the absorption of the distal part of the tentacle.

In the strobila shown in Fig. 24, the rhopalial tentacles have a very different appearance from what we have seen before. They are shorter than the other tentacles, and are much swollen at a point just beyond the eye-spot. The distal portion is beginning to degenerate. This process, when once begun, proceeds rapidly. During the few hours that were spent in making this drawing, the rhopalial tentacles were reduced in length nearly one half. The eye-spots and concretions were conspicuous, and in each of the former there was a slight cup-shaped depression. This is the earliest stage in which I observed slight medusa-like movements of the ephyra disc. The tentacle at this stage is in a process of degeneration for about fifteen hundredths of a millimeter outward from the ocellus. In this area of degeneration (*t.* Fig. 55) the endodermal cells are broken down, the supporting membrane has disappeared, and the inner boundary of the ectoderm is indistinct. The axial mass of this part of the tentacle is made up of loose particles of a finely granular substance, in which may be seen many small and deeply stained nuclei. There are also a number of green cells that apparently escaped into the central mass when the supporting membrane broke down. There is evidently a free communication between this mass of disintegrating material and the digestive cavity, through the rhopalial canal.

The method by which the shortening of the tentacle is brought about would seem to be as follows: The axial cells adjoining the cells that bear the concretions (Fig. 54) first break down. Why they should do so, and at this particular time, I cannot say. This disintegration proceeds centrifugally, and it is accompanied by a dissolution of the supporting membrane. The ectodermal cells then either begin here and there to break down while still in place, and the resulting debris is squeezed into the central cavity; or else, the cells migrate, or are squeezed inward and then disintegrate. The continuity of the remaining ectoderm is maintained, however. The products of degeneration probably pass through the rhopalial canal into the digestive tract. As this process continues, the inward movement of the ectodermal cells is more rapid than their disintegration, so that when the distal part of the tentacle is reduced to the size of the rhopalial part (Figs. 25 and 55), it is a solid mass of small cells with small nuclei that stain dark. Some of these cells contain a large vacuole and have the nucleus pushed to one side. Scattered among the small cells, there are a number of globular bodies as large as, or larger than, the green cells, and completely filled with coarse granules that stain deeply with safranin; no nucleus is visible in them. The ocellus has now become distinctly cup-shaped (*oc.* Fig. 55).

At about this time the interrhopalial tentacles begin to be absorbed in their turn (Fig. 25). The umbrellar margin has in the mean time grown out beyond the insertion of each interrhopalial tentacle, on its aboral side, into two lobes with a hood between (Figs. 25 and 26). This structure, although smaller, corresponds exactly to the rhopalial lobes and hood, and is further evidence for the homology between the tentacles and the rhopalia. The drawing reproduced in Fig. 25 was made between the hours of eleven in the morning and two in the afternoon. At five o'clock of the same day the tentacles had been reduced to one third the length shown in the figure, and the absorption of the rhopalial tentacles was very nearly completed.

In the later stages of the absorption of the interrhopalial tentacles, the broken-down material is evidently forced in some way into the radial canal. The rhopalium (Fig. 56) is practically complete at this stage. The point (x) where the last trace of the tentacle proper disappeared, is still distinguishable in sections by the presence of small cells with indistinct cell walls, and by the absence of otoliths.

These observations, then, confirm those of Claus ('**83**,) who, without going into the details of development, maintained that the rhopalia are modified basal portions of the tentacles of the scyphistoma; and they contradict Goette's statement that the rhopalia are developed independently of the tentacles.

Other Phenomena of Strobilization.— While the marginal structures are undergoing the metamorphosis that has just been described, important alterations are taking place in the general shape of the body. The horizontal constriction first noticed in Fig. 21 has deepened (Fig. 24), while the fold below it has heightened, and the upper portion has broadened and flattened, until the condition shown in Fig. 26 is reached. At this final stage the upper portion has all the characteristics of a free-swimming medusa (ephyrula), except that it is attached by a slender aboral stem to the centre of a goblet-shaped basal polyp. The four interradial depressions in the peristome of the earlier stages have become nearly flattened out, all that remains of them being the hollows between the projecting radial angles, or pillars, of the proboscis, which have now become very prominent.

At the stage of Fig. 21, there may be noticed on the proboscis eight patches of thickened ectoderm containing many nettle cells. These nettle batteries are arranged symmetrically, one on each side of each pillar of the proboscis. At a little later stage (Fig. 24) the batteries have become invaginated, forming cup-shaped depressions, thickly crowded with nettle cells in all stages of development.

During the time when the larva is being differentiated externally into an upper and a lower portion, internal changes are taking place in the former, which result in the disappearance of structures characteristic of the scyphistoma and the appearance of others distinctive of the medusa.

The orifices in the gastric septa have become relatively larger (*cs.* Fig. 52 and *rc.* Fig. 57) until the septa are reduced to columnar pillars, columellae, connecting the upper and lower walls of the body and pierced longitudinally by the septal muscles (c. Fig. 58). The columellae are called by German authors "Septalknoten," but they are not homologous with the so-called "Septalknoten," or areas of adhesion, in the Peromedusae. The columellae of the Peromedusae are the walls of the large septal funnels where they pass from the subumbrella to the exumbrella, and, according to Haeckel's figures, are separated by the gonads from the areas of adhesion.

In the fully developed scyphistoma of Cassiopea, the septal muscles are solid throughout their length, and there is no cavity corresponding to the septal funnels, which, according to Goette, are well developed in Aurelia. But in the strobila there does appear a slight depression extending a very short distance into the end of each septal muscle. In Figs. 57 and 58, where this is well marked, much of the depression may be due to the strongly contracted condition of the specimens; but other specimens not so contracted show at least the deeper part of the cavity, which therefore, may be truly a vestige of the septal funnel.

At an early stage of strobilization there may be noticed a short conical projection from the central edge of each columella. It extends also around the sides. These projections are probably the rudiments of the first four gastric filaments, which are distinctly developed at the time when the ephyrula is set free (*cf.* Fig. 58).

While the septa are shrinking to become the columellae, ridges appear opposite each other on the upper and lower walls of the peripheral part of the digestive tract between the bases of the tentacles. The epithelial membranes at the summits of opposite ridges unite, and thus there is formed a series of lines of adhesion extending inward from the periphery and dividing the space into a series of radial canals, each ending in a tentacle. The two discs of mesogloea never fuse along these lines of adhesion, but the endoderm remains between them as the endodermal lamella, or cathammal plate. At the stage of Fig. 24 the lines of adhesion occupy about half the space from the margin to the columellae.

The lower disc of the strobila remains simply an annular fold of the body wall until the metamorphosis of the upper disc is nearly complete. The septal muscles in this region bend outward with the rest of the body wall (Fig. 57). At length, however, the endoderm grows out toward the periphery as four shallow pouches, leaving septa between them which contain the longitudinal muscles. Very soon after this the septa are perforated so as to allow a fusion of the endoderm at their upper angles (Fig. 58). In the last stage of strobilization (Figs. 26 and 59) the longitudinal muscles may be traced from the peristome through the columellae and the mesogloea of the exumbrella to the narrow isthmus where the ephyrula disc joins the basal polyp. The latter has now a well-developed peristome (Fig. 59), and the mesogloea in this region is very thin. Just in the isthmus the muscles have disappeared, but they may be found again in the peristome of the basal polyp and traced for a distance close under the epithelium to the edges of the septa, where they bend abruptly downward, and continue through the septa into the stem.

Although seldom visible in the living specimen, sections show that the basal polyp at this stage possesses eight short tenacles (Fig. 59). It has also an annular fold of the ectoderm, closely surrounding the isthmus (Fig. 59 and *p.* Fig. 60). This fold is the rudiment of a new proboscis, which is without doubt entirely ectodermal in origin. But, as Goette has pointed out, it does not follow from this that the lining of the proboscis is ectodermal in scyphistomas developed from the egg. Pulsating contractions of the umbrella are first noticed at the time when the rhopalial tentacles begin to be absorbed (Fig. 24). They are then feeble and at long intervals. At the stage of Fig. 26 these movements are rapid and violent. The rhythm is interrupted by few pauses, and these are short. The result of these movements is that the thin wall of the isthmus is ruptured, and the ephyrula is set free.

After this separation, the basal polyp has the appearance represented in Figs. 27 and 28. It is a scyphistoma with seventeen short tentacles and a rudimentary proboscis (Figs. 61 and 62). The proboscis and the tentacles grow rapidly, so that in a few days it is impossible to distinguish a regenerated basal polyp from a young scyphistoma in the sixteen-tentacle stage, except that the former has a somewhat thicker stem. It may be inferred from this complete regeneration of the basal polyp that it undergoes repeated strobilization, as Claus[1] has found to be the case in Aurelia.

The Ephyrula. — The ephyrula of Cassiopea is very different in appearance from the corresponding stage in ordinary scyphomedusae with eight rhopalia. Cotylorhiza has an ephyrula resembling the same stage in the semostomatous medusae. Good figures of this are given by du Plessis and Claus, and there is a striking difference between these figures and Figs. 29 and 30 in this paper, which are camera drawings of well-preserved ephyrulas of Cassiopea, mounted in balsam. Fig. 29 represents a young Cassiopea that has not long enjoyed a free existence. The general shape of the umbrella is like that of the adult, and there is the same concavity in the centre of the exumbrella, while the margin curves in the opposite direction, as in Fig. 64. The typical ephyrula of Aurelia or Cotylorhiza has eight marginal arms with two lobes at the end of each, and between each pair of lobes there is a rhopalium. In Cassiopea structures corresponding to these arms are present to the number of sixteen, or often more. But these do not destroy the general circular outline of the animal, for they are connected by thin areas on the umbrella, alternating with an equal number of ridges, which at an earlier stage bore the interrhopalial tentacles on their under sides.

We have, then, at this stage the marginal zone of the umbrella marked by a number of short radial ridges separated by an equal number of thin areas. The ridges are in line with the radial canals. At the peripheral end of each ridge the margin of the umbrella is produced into two lobes, those adjoining the rhopalia being well marked, the others small and inconspicuous (*il.* Fig. 30).

In Fig. 29 there are seventeen, and in Fig. 30, twenty-three, rhopalia. The latter is an unusually large number, and it will be noticed that the number of marginal lobes has not increased in proportion, so that irregularities of the margin occur in many places, as described in the section on variations.

At this stage the rhophalia have come to lie, as in the adult, wholly within the margin of the umbrella, and project from its subumbrellar surface. The interrhopalial tentacles have totally disappeared. The lines of adhesion separating the radial canals are faintly visible as radiating lines of greater transparency.

---

[1] See foot-note, Claus ('92).

The four lips of the mouth are spread out into a cross-shaped figure, and one may look directly through the lumen of the oesophagus into the stomach and see the four gastric filaments (Figs. 29 and 30). Each one of the four lips is nearly square, and from its two outer angles there are two grooves that extend obliquely inward until they meet and form a V. The point of the V is in an angle of the oesophagus, along which there is a groove that is continuous with the other two grooves, and that extends into the stomach. On the interradial side of each of the eight labial grooves, there may be seen a small roughly circular area that is less transparent than the rest. These areas are the nettle batteries, first seen in the strobila. The margins of the lips are provided with numerous small processes, the digitella, which are arranged in a single continuous series.

Fig. 63 is a section of an ephyrula that has just become free. In this stage there is still an opening through the aboral wall of the stomach, and one may see the last vestige of the connection between the columella and the exumbrella, which contains also the degenerating remnants of the septal muscle.

At a little later stage, when the opening in the roof of the stomach has closed, both the septal muscles and the septal funnels totally disappear. Sometimes one, sometimes the other, is the first to vanish.

The Later Stages.—The later stages in the development of Cassiopea will be treated very briefly. While the umbrella remains at first unchanged, the metamorphosis of the mouth parts is inaugurated by the growth of the two outer angles of each of the more or less quadrate lips, so that they are soon drawn out into extended lobes (Fig. 31). At the same time the pillars of the proboscis thicken, and the mesogloea is continued outward along each of these lobes as a midrib. We have then eight oral arms, each with a longitudinal groove, supported by a midrib, and fringed with digitella,—arms very similar to those characteristic of the genus Aurosa Haeckel ('79). But it is only the mouth parts of Cassiopea that may be said to pass through an Aurosa stage, for the comparison cannot, at this time at least, be carried to the other organs.

Claus has described ('83) some of the principal stages in the metamorphosis of Pilema (Rhizostoma) and Cotylorhiza. He regards the formation of the eight oral arms as a different process in these forms from what occurs in Aurosa. But it appears to be merely the same thing expressed differently.

In the next stage we find two oral funnels, or oscula, and a small vesicle developed at the tip of each oral arm. The other portions of the arm are still open and fringed with digitella, as before, but the outline is no longer a regular curve, for there are folds in the margin. The deepest folds are the most distal, and they become progressively more shallow toward the base of the arm. The central mouth is still widely open. The subgenital cavities are well developed at this stage. Figs. 64, 65, and 66 show how the oral disc is formed, and how the subgenital cavities are produced by the great increase in thickness of the mesogloea at the pillars of the proboscis and the bases of the oral arms. By the growth of these structures, the subgenital cavities are necessarily produced. The only special adaptations are the subsequent growth and folding of the aboral wall and the narrowing of the orifice.

The marginal lobes of the umbrella now begin to broaden, and thus approach the adult condition, but there is only a single " vellar " lobe between two rhopalial ones.

At a little later stage, when there are three oral funnels at the tips of the arms (Fig. 33), the re-entrant angles between the pillars of the proboscis have grown inward, met at the centre, and fused. In this way the lumen of the oesophagus is divided into four tubes (Fig. 32), representing the grooves that were present in its angles in the earlier stages. In the figure the fusion at the centre has gone so far as to involve the edges of the lips, and the labial grooves of the different pairs of arms are not in open communication, but a short cross-shaped tube connects them at the centre, and the oral disc is now completed.

It is interesting to note that Claus has found a stage both in Pilema and in Cotylorhiza that, while showing the characteristic family differences, has also a certain resemblance to this stage in Cassiopea. In all three the walls of the proboscis have fused so as to divide its lumen into four tubes, and the formation of oscula has begun at the tips of the arms in such a way that we have on each arm three oscula with a vesicle in the angles between them. The occurrence of this stage in the ontogeny of three so distinctly separated families must have some morphological significance, and we may regard these eight primary vesicles as homologous in the three groups.

The mode of formation of the oral funnels becomes evident at this stage. They are not formed in Cassiopea simply by a series of fusions of the lips along the line of the labial groove, as Hamann (**'81**) states to be the case in Cotylorhiza. It is more like the process in Pilema, as described by Claus. Each of the primary funnels is represented at first by one of the folds in the margin of the lips referred to above (Fig. 33). The fold deepens, and its edges are brought together on the ventral side and fuse, leaving an opening at the apex of the fold, the osculum. At the same time the labial groove in this region is converted into a canal by the fusion of the lips on its two sides. After the fusion all trace of what has occurred quickly disappears.

With the division of the oesophagus into four tubes, and the completion of the oral disc, our larva comes to be distinctly a rhizostomatous medusa. Further development of the mouth parts consists in the continued division of the labial, or brachial, grooves into oral funnels and brachial canal, together with the development of oral vesicles. By the time two or three vesicles have been formed on the end of each arm, a vesicle appears in the centre of the oral disc. Except for this interruption, the development of the mouth parts proceeds regularly in a centripetal direction. The funnels and vesicles are formed first at the tips of the arms, and then one after another in regular succession toward the centre. Each of these primary funnels is the rudiment of one of the primary branches of the arm. When the process of forming funnels has reached about half the length of the arm, the distal funnels begin to subdivide. By this subdivision of the primary funnels new ones are produced, of which some are the rudiments of secondary branches; these subdivide again, and so on, as long as growth continues. The subdivision is not dichotomous, but takes place in such a way as to produce alternate branches. The formation of a vesicle takes place at this stage in some way at about the time of the completion of the adjoining funnel. I have not been able to determine whether the vesicle is a funnel with the orifice closed, as Hamann claims it to be, or whether it is an evagination from the pedicle of a funnel, as at first it seemed to me to be, and as Claus thinks it probably is.

According to Haeckel ('79), the genus Archirhiza represents a form that was the ancestor of all the rhizostomatous medusae. Of this genus there are two known species, *A. primordialis* Haeckel, and *A. aurosa* Haeckel. They agree in having four subgenital cavities and eight simple unbranched arms that are provided with a single zig-zag row of closely set oral funnels, and are devoid of other appendages. Hamann says that a stage representing this condition is a feature of the ontogeny of rhizostomatous medusae. From what has been said it is evident that we have no such stage in the development of *Cassiopea xamachana*, for while the labial groove is still open in the proximal half of the oral arm, in its distal half the vericles are formed, and branches are in the process of formation.

The outline of the umbrellar margin has not changed essentially since the last stage. The areas of adhesion have become much wider than the radial canals they separate, and in them there has appeared a network of anastomosing canals, while the gastric filaments have become numerous.

We have now followed the larva of our Cassiopea from its first appearance as a bud to a point where, with the exception of the gonads, all the organs of the adult are outlined. Here we must take leave of it.

SUMMARY AND CONCLUSIONS.

Cassiopea and Polyclonia are genera of rhizostomatous medusae peculiarly modified in adaptation to a sedentary mode of life in shallow water among the mangroves bordering tropical seas. A comparison of specimens of *Polyclonia frondosa* Ag. with *Cassiopea xamachana* shows that these two forms are specifically distinct, although in general appearance they are very similar and they have the same geographical range and habitat.

C. xamachana is remarkable for its variability. This is especially shown in the appendages to the mouth parts and in the structures at the margin of the umbrella. It will be noticed that the most frequent number of rhopalia, in the twenty-seven specimens examined, was sixteen, which is the typical number for the genus. But the variations are not arranged symmetrically on the two sides of this mode, for specimens having a greater number of rhopalia are more than twice as many as those having less. The species shows a strong tendency toward duplication of the rhopalia and associated structures of the umbrella; and at the same time the symmetrical relations of the parts tend to be preserved. The great majority of scyphomedusae have only eight rhopalia, and in Cassiopea with its sixteen rhopalia we have a beautiful illustration of Darwin's law that "A part developed in any species in an extraordinary degree or manner, in comparison with the same part in allied species, tends to be highly variable." Study of the color markings and measurements of the mouth parts indicates the division of the species into three varieties; and it was in one of these, var. *A*, that the duplication of marginal organs was especially prevalent.

The color of both larvae and adults is due to a great extent to the presence in the mesogloea of minute symbiotic algae. That these are plant cells was demonstrated by micro-chemical tests. Their presence undoubtedly enables the medusae to live in water that would be too poor in oxygen for most marine animals.

The search for developing eggs proved unsuccessful, but scyphistoma larvae were abundant, and it was found that they were multiplying rapidly by budding.

The bud arises as an evagination of the body wall of the scyphistoma. There is no evidence of any special gemminal epithelium. The bud, when set free, differs from a planula chiefly in the possession of a well-defined mesogloea and four septal muscles. The septal muscles are shown to be formed as branches of the two adjacent septal muscles of the parent. The mouth of the young scyphistoma is formed by a minute perforation at the former point of attachment, while the distal end of the bud becomes the stem. This remarkable orientation agrees with what Goette and Claus have found in Cotylorhiza. In the formation of the mouth there is no evidence of any invagination of ectoderm. Apparently the oesophagus, as well as the gastric pouches, is lined with endoderm. On the other hand, the oesophagus of the lower disc of the strobila is formed wholly of ectoderm.

The four radial tentacles are formed simultaneously, and the four interradial ones appear at the same time or slightly later. These are followed by eight adradial tentacles and sixteen more are added a little later, making thirty-two in all. It was found that the rudiments of the interradial tentacles are not at all constant in position with relation to the septa. Some were septal, others were interseptal, sometimes on one side of the septum, sometimes on the other, thus agreeing with the observations of Claus on Aurelia and Cotylorhiza.

The four gastric pouches are formed at the same time by the ingrowth of the septa. They are soon brought into communication at the periphery by the perforation of the septa, which become reduced to columellae surrounding the longitudinal muscles.

Contrary to Goette's opinion, it may be stated positively that the rhopalia are differentiated in the bases of alternate tentacles. After the rhopalium is fully developed, the distal part of the tentacle undergoes degeneration and is absorbed. The development was traced for the first time through all its stages, and the opinions of Agassiz, Claus, and Lendenfeld are fully confirmed.

The scyphomedusae are the only coelenterates, which possess four longitudinal muscles of ectodermal origin completely imbedded in the mesogloea between the points of insertion. The buds of Cassiopea have this distinctively medusoid characteristic long before they are detached. Moreover, the methods by which the mouth and the gastric pouches are formed differ entirely from what is said to take place in larvae that pass through an anthozoan stage. Therefore, whatever may be true of the larvae derived from eggs, this stage is certainly omitted in larvae produced by budding.

The first step toward the formation of the free-swimming medusa is the perforation of the gastric septa which takes place in the young scyphistoma before it is fully developed. Then follows a period of growth and reproduction by budding, and further metamorphosis begins finally with the process of strobilization. Besides the differentiation of the sense organs and the development of the marginal lobes of the umbrella, the most important events are the development of the angles of the mouth into quadrate lobes and the fusion of the two layers of endoderm along certain areas of adhesion so as to divide the periphery of the digestive tract into a series of radial canals. Only one medusa is formed; but, separated from this by a constriction, is a small basal segment which, a short time before the medusa becomes free, begins to develop gastric pouches, tentacles, and a proboscis. This becomes eventually a perfect scyphistoma, and after a period of growth probably undergoes strobilization again.

There has been considerable discussion in regard to the nature of strobilization; the question being whether the medusa is to be regarded as a metamorphosed scyphistoma, or as derived from the scyphistoma by a process of budding. In the monodiscous strobila of Cassiopea we have clearly a metamorphosis. The form of the medusa is the result of a series of changes which begin very early and involve all the essential organs of the scyphistoma. The portion not involved in these changes merely serves as a mechanical support. That this part is separated off and regenerates the lost parts, instead of being absorbed, may be regarded as merely an incidental fact.

If there be any question of budding it refers to this basal segment. And this suggests a striking analogy between the basal polyp and the peculiar planula-like buds. In the first place they have the same orientation relative to the upper disc. In both, the distal end forms the stem and the proximal end forms the mouth. In the second place, they have essentially the same structure. Each one consists of a simple sac with a wall made up of three layers, ectoderm, mesogloea and endoderm, and each is provided with four longitudinal muscles imbedded in the mesogloea. What differences appear in the subsequent development, may be attributed to the different ways in which the two become separated from the disc and to the greater size of the longitudinal muscles in the basal polyp. The production of supernumerary tentacles, rhopalia, and marginal lobes, is common in this species. Why may we not regard the buds as supernumerary basal polyps, and their subsequent development as a process of regeneration preserved and modified by natural selection for its obvious advantage?

The ephyrula of Cassiopea has the same number of rhopalia as the adult, and differs in shape from the corresponding stage of ordinary scyphomedusae with eight parameres.

The most important event in the later stages is the metamorphosis of the mouth parts. The angles of the four quadrate lips become extended to form eight oral arms somewhat similar to those found in the adult Aurosa. There is no Archirhiza stage, but there follows a stage with the oesophagus divided into four tubes, and with three oscula and an oral vesicle on each arm. A similar stage has been found in Pilema and Cotylorhiza, and it may have some phylogenetic significance.

The studies of numerous investigators upon the Ascidians have demonstrated that a knowledge of the gamogenetic development of an animal will not always enable one to predict how the organs will be formed in the agamogenetic process. So it may be objected that the results set forth in this paper do not afford a valid basis for the criticism of work done by others on larvae developed from the egg. On the other hand, the eight-tentacle stage of the bud larva of Cassiopea is so like the same stage of the sexually produced larva of its near relative Polyclonia that it would be impossible to tell them apart, and, in the absence of any evidence to the contrary, there seems to be no necessary reason for supposing that their later history is different. At any rate, we have here the first fairly complete history of the development of a scyphomedusa from the bud, and when the sexual development of *Cassiopea xamachana* or an allied species is studied, this memoir will serve as a means of comparison, and will make it possible to determine whether or not the two modes of ontogeny are alike.

Literature.

Agassiz, A.

'65 North American Acalephae. Illustrated catalogue of the Museum of comparative zoology at Harvard College. No. 2, 1865, p. 41.

'81. Polyclonia frondosa. Nature, vol. 24, 1881, p. 509.

Agassiz, A., & Mayer, A. G.

'99. Acalephs from the Fiji Islands. Bull. mus. comp. zool., vol. 32, no. 9, 1899. Description of [illegible]

Agassiz, L.

'60. Contributions to the natural history of the United States of America. Vol. 3 and 4. Boston, 1860.

Archer, H.

'81 Medusae. Nature, vol. 24, 1881, p. 307.

Berger, E. W.

1900 Physiology and histology of the Cubomedusae, including Dr. F. S. Conant's notes on physiology. Mem. biol. lab. Johns Hopkins Univ. vol. 4, no. 4.

Bigelow, R. P.

'90 The marginal sense organs in the Pelagidae. Johns Hopkins Univ. circ., vol. 9, 1890, no. 80, p. [illegible]

'92a On reproduction by budding in the Discomedusae. J. H. U. circ., vol. 11, 1892, no. 97, p. [illegible]

'92b On the development of the marginal sense organs of a rhizostomatous medusa. J. H. U. circ., vol. 11, 1892, no. 97, p. 84.

'92c. On a new species of Cassiopea from Jamaica. Zool. Anz., Jahrg. 15, 1892, no. 393, pp. 212–214.

'93. Some observations on Polyclonia frondosa. J. H. U. circ., vol. 12, 1893, no. 106, p. 106.

Brandt, J. F.

'38. Ausführliche Beschreibung der von C. H. Mertens auf seiner Weltumsegelung beobachteten Schirmquallen. Mém. Acad. imp. sci. St. Petersbourg, sci. math. phys. et nat., (6) vol. 4 (pt. 2, sci. nat., vol. 2), 1838, pp. 394–399.

Brooks, W. K.

'86 The life history of Hydromedusae, a discussion of the origin of medusae and the [illegible] Mem. Boston soc. nat. hist., vol. 3, no. 12, 1886; also Mem. biol. lab. Johns Hopkins Univ., vol. 1.

Claus, C.

'77 Studien über die Polypen und Quallen der Adria. Denkschr. d. math.-naturw. Classe d. k. Akad. d. Wissenschaften, Wien, Bd. 38, 1877.

'81. Ueber einige bislang noch unbekannte Larvenstadien von Rhizostoma. Zool. Anz., 1881, No. 76, p. 79.

'83. Untersuchungen über die Organisation und Entwicklung der Medusen. Prag und Leipzig, 1883, 96 pp., 20 pl.

'84. Die Ephyren von Cotylorhiza und Rhizostoma. Arb. zool. Inst. Wien, vol. 5, 1884, p. 169.

'90. Ueber die Entwicklung des Scyphostoma von Cotylorhiza, Aurelia, und Chrysaora. Arb. zool. Inst. Wien, vol. 9, 1890, p. 29.

'92. Ueber die Entwicklung des Scyphostoma von Cotylorhiza, Aurelia und Chrysaora, sowie über die systematische Stellung der Scyphomedusen, II. Arb. a. d. zool. Inst. d. Univ. Wien, vol. 10, 1892, pp. 1–70.

du Plessis, G.

'81. Remarques sur les metamorphoses de la Cassiopée bourbonnienne. Bull. soc. vaudois, Lausanne, ser. 2, vol. 17, 1881, p. 633.

Fewkes, J. W.

'82. Notes on acalephs from the Tortugas, with description of new genera and species. Bull. mus. comp. Zool., vol. 9, no. 7, 1882.

Fischer, P.

'88. Note sur des scyphistomes de méduse acraspède. Bull. soc. zool. de France, vol. 13, 1888, p. 96.

Forskål, P.

1775. Descriptiones animalium . . . . quae in itinere orientali observavit. Hauniae, Möller, 1775, p. 107.

1776. Icones rerum naturalium, quas in itinere orientali depingi curavit. Hauniae, 1776, pl. 31.

Frantzius, A. v.

'53. Ueber die Jungen der Cephea (Cotylorhiza.). Zeitschr. f. wiss. Zool., Bd. 4, 1853, p. 118.

Goette, A.

'87. Entwicklungsgeschichte des Aurelia aurita und Cotylorhiza tuberculata. Hamburg and Leipzig, 1887.

'91. Claus und die Entwicklung der Scyphomedusen. Leipzig, 1891.

'93. Vergleichenden Entwicklungsgeschichte von Pelagia noctiluca Pér. Zeitschr. f. wiss. Zool. Bd. 55, 1893, pp. 645-695. [Die Larven von Cotylorhiza tuberculata L., pp. 645–659.]

Gray, J. E.

'69. Habits of the Medusae. Annals and mag. nat. hist., ser. 4, vol. 4, 1869, p. 295.

Guppy, H. B.

'82. Habits of Scyphomedusae. Nature, vol. 27, 1882, p. 31.

Haacke, W.

'85. Pseudorhiza Haeckelii spec. nov., der Endspross des Discomedusenstammes. Biol. Centralb., vol. 4, 1885, p. 291.

Haeckel, E.

'69. Crambessiden. Zeitschr. f. wiss. Zool., vol. 19, 1869, p. 509.

'79. Das System der Medusen. Jena, 1879.

'81a. Report on the deep sea medusae. Challenger reports, zool., vol. 4, 1881.

'81b. Metagenesis and Hypogenesis von Aurelia. Jena, 1881.

Hamann, O.

'81. Die Mundarme der Rhizostomen und ihre Anhangsorgane. Jenaische Zeitschr. f. Naturw., vol. 15, 1881, p. 243.

Hertwig, O. & R.

'78. Das Nervensystem und die Sinnesorgane der Medusen. Leipzig, 1878.

'79. Die Actinien. Jena, 1879.

Hesse, R.

'95. Ueber das Nervensystem und die Sinnesorgane von Rhizostoma cuvieri. Zeitschr. f. wiss. Zool., vol. 60, 1895, p. 411.

Hyde, Ida H.

'94. Entwicklungsgeschichte einiger Scyphomedusen. Zeitschr. f. wiss. Zool., vol. 58, 1894, p. 531-565.

Keller, C.

'83. Untersuchungen über neue Medusen aus dem Rothen Meere. Zeitschr. f. wiss. Zool., vol. 38, 1883, p. 621.

Lacaze-Duthiers, H. de.

'93. Scyphistome. Archives de zool. expér., ser. 3, vol. 1, 1893, notes et revues, p. xxx.

Lamarck, J. B. de

'37. Histoire naturelle des animaux sans vertébres. Ed 3. Paris, 1837, vol. 1, p. 457.

Lang, Albert.

'92. Ueber die Knospung bei Hydra und einigen Hydropolypen. Zeitschr. f. wiss. Zool., vol. 54, pp. 363–385.

Lendenfeld, R. v.

'82. Ueber eine Uebergangsform zwischen Semostomen und Rhizostomen (Pseudorhiza). Zool. Anz., Jahrg. 5, 1882, p. 380.

'84. Zur Metamorphose der Rhizostomen. Zool. Anz., Jahrg. 7, 1884, p. 429.

'88. Die australischen rhizostomen Medusen. Zeitschr. f. wiss. Zool., vol. 47, 1888, p. 201.

McMurrich, J. P.

'91. The Development of Cyanea arctica. Amer. nat., vol. 25, 1891, p. 287.

Metschnikoff, E.

'86. Embryologische Studien an Medusen. Wien, 1886.

Milne-Edwards, H.

'49. Les zoophytes. Cuvier, Regne animal illustré. Vol. 10, 1849, pl. 51.

Reid, J.

'48. Observations on the development of the medusae. Annals and mag. nat. hist., ser. 2, vol. 1, 1848, p. 25.

Sars, M.

'41. Ueber die Entwicklung der Medusa aureta und Cyanea capillata. Arch. f. Naturg., vol. 7, 1841, p. 9.

Schewiakoff, W.

'89. Beiträge zur Kenntnis der Acalephenauges. Morph. Jahrb., vol. 15, 1889, p. 25.

Schneider, A.

'70. Zur Entwicklungsgeschichte der Aurelia aurita. Arch. f. mik. Anat., vol. 6, 1870, p. 363.

Schultze, L. S.

'98. Rhizostomen von Ternate. Abh. senckenb. naturf. Ges., vol. 24, 1898, p. 153. [Occurrence of *Cassiopea* sp.?]

Smith, Frank.

'91. The gastrulation of Aurelia flavidula Pér. & Les. Bull. mus. comp. zool., vol. 22, no. 2, 1891.

Tilesius, W. G. v.

'29. Zur Naturgeschichte der Medusen. Nova Acta Physico-Medica, N. C., vol. 15. 1829, p. 266.

Vanhöffen, E.

'88. Untersuchungen über semaeostome und rhizostome Medusen. Leuckart & Chun's Biblioth. Zool., Heft 3, 1888.

EXPLANATION OF PLATES.

All the figures from 1 to 28, and Figs. 34 and 35, are freehand drawings made from the living animals. Figs. 29 to 33 are from well-preserved specimens mounted in balsam, and were outlined with the camera lucida. The remaining figures, except Fig. 37, are camera-lucida drawings of microtome sections. All the figures are reduced uniformly to slightly less than one half the diameter of the original drawings.

LETTERING COMMON TO ALL THE FIGURES.

b. — bud.
c. — columella.
c d. — circum-oral disc, or peristome.
c s. — circular sinus.
cx. — calyx.
d. — digitellum.
ect. — ectoderm.
e l. — endodermal lamella, or cathammal plate.
end. — endoderm.
e u. — exumbrella.
g. — stomach.
g f. — gastric filament.
g p. — gastric pouch.
h. — hood.
i l. — interrhopalial lobe.
i t. — interrhopalial tentacle.
l g. — labial groove.
m. — mouth.
mes. — mesogloea, or supporting membrane.
n f. — nerve fibres.
o a. — oral arm.
oc. — ocellus.
o d. — oral disc.
oe. — oesophagus.

oe. t. — oesophageal tube, or canal.

os. — osculum.

ot. — rhopalial concretion (otolith).

p. — proboscis.

p. p. — pillar of the proboscis.

r. c. — radial canal.

rh. — rhopalium.

rh. c. — rhopalial canal.

rh. t. — rhopalial tentacle.

s. — stem.

s. e. — sensory epithelium.

sep. — septum.

s. f. — septal funnel.

s. g. — subgenital cavity.

s. m. — septal muscle.

s. u. — subumbrella.

t. — tentacle.

v. — vesicle.

za. — brownish green cells, symbiotic algae.

PLATE 31.

Fig. 1. Portion of the calyx and stem of a scyphistoma with a fully developed bud (*b*) attached. *A*, the outline of the same bud when contracted.

Fig. 2. Similar to the preceding, except for the formation of a second bud (*b′*) which bears the older one (*b*) upon its apex.

Fig. 3. The form of the planula-like bud during the first two days after becoming free. *A*, *B*, and *C*, are the successive changes in shape observed in one specimen during a few minutes. The arrows show the direction in which it swims.

Fig. 4. Larva of probably the third day. *A*, lateral aspect; *B*, oral aspect.

Fig. 5. A larva of about the same age, 48 hours or over.

Fig. 6. Another larva of 48 hours or over.

Fig. 7. Larva of the fourth day.

Fig. 8. Free scyphistoma of the fifth day, with rudiments of four tentacles. The arrows show the direction of progression and rotation.

Fig. 9. A scyphistoma of about the same age, with the rudiments of eight tentacles.

Fig. 10. Oral aspect of a similar larva, perhaps somewhat younger.

Fig. 11. A scyphistoma a little more advanced, probably in the fifth day.

Fig. 12. A still more advanced scyphistoma of the fifth day. The four tentacles first formed are much longer than the other four.

Fig. 13. Scyphistoma of the sixth day, attached, and with eight tentacles.

Fig. 14. Scyphistoma with rudiments of the second set of eight tentacles. Two tentacles of the first series are bifurcated.

Fig. 15. Scyphistoma with sixteen tentacles fully developed, in the attitude of feeding.

Fig. 16. Oral aspect of a similar specimen.

PLATE 32.

Fig. 17. Scyphistoma showing first traces of rhopalial structure.

Fig. 18. A small portion of the margin more highly magnified.

Fig. 19. Scyphistoma at a slightly older stage.

Fig. 20. Small part of the margin of a similar larva.

Fig. 21. An early stage in strobilization.

Fig. 22. A rhopalial tentacle of the same specimen seen from the side.

Fig. 23. An older rhopalial tentacle.

Fig. 24. Strobila in which the rhopalial tentacles have begun to degenerate.

PLATE 33.

Fig. 25. Strobila, in which the degeneration of the rhopalial tentacles is nearly completed, and the interrhopalial tentacles have begun to degenerate.

Fig. 26. A complete strobila. The basal polyp bears a bud which broke off and swam away while the drawing was being made. The ephyrula was detached during the following night. The rhopalia are visible through the umbrella. At *y*, is a pair of twin rhopalia, compare *y*, Fig. 30.

Fig. 27. The basal polyp of the same specimen, a few hours after the separation of the ephyrula.

Fig. 28. Optical section of the same.

Fig. 29. An ephyrula recently set free. Oral aspect. The gastric filaments are visible through the mouth. × 31.

Fig. 30. A specimen of about the same age, showing variations of the margin at *u*, *w*, *x*, *y* and *z*. × 31.

PLATE 34.

Fig. 31. Mouth parts of a young medusa in the Aurosa stage. The gastric filaments may be seen through the central mouth opening. × 33.

Fig. 32. Oral disc of an older specimen. The oesophageal tubes appear as light areas, one at the junction of each pair of labial grooves.

Fig. 33. One of the oral arms from the same specimen as Fig. 32.

Fig. 34. Floor of the stomach and the oral arms of an adult, viewed from the aboral side. The roof of one subgenital cavity is removed, and a thread is represented as passing through the external orifice into this cavity, at *x*. The ultimate branches are represented on only one of the oral arms.

Fig. 35. Portion of the aboral surface of an adult. About half natural size.

PLATE 35.

Fig. 36. Section of a young bud. × Zeiss DD + oc. 2.[1]

Fig. 37. Diagram to show the branching of the septal muscles, sm_1, sm_2, sm_3 and sm_4, and the connections of the septal muscles of the bud, sm'_1, sm'_2, and sm'_3. Reconstructed from the series of sections of which Fig. 36 is one.

Fig. 38. Section through the distal apex of an older bud, showing the attachment of a septal muscle to the ectodermal epithelium. × Zeiss H + oc. 2.

Fig. 39. Longitudinal section of a planula-like larva. *D* was the distal, and *P* the proximal, end of the bud while attached. × Zeiss DD + oc. 2, dt. 160.

Fig. 40. Longitudinal section through the posterior end of a swimming larva, in which changes preparatory to the formation of the mouth are taking place. × B & L $\frac{1}{8}$ + Zeiss oc. 2.

Fig. 41. Similar section of a slightly older larva, showing the mouth as a small opening not exceeding in width the thickness of the section. × B & L $\frac{1}{8}$ + Zeiss oc. 2, dt. 160.

Fig. 42. Adradial section of a scyphistoma a little older than Fig. 9 (5th day). × Zeiss DD + oc. 2.

Fig. 43. Obliquely transverse section of a specimen of the same age, showing the greatest width of one septum. × B & L $\frac{1}{8}$ + Zeiss oc. 2, dt. 160.

Fig. 44. A tangential section of an older larva, showing the connection of a septal muscle with the circum-oral disc. × Zeiss H + oc. 2.

PLATE 36.

Figs. 45 to 47 are consecutive transverse sections of one individual. Fig. 45 shows the continuity between the endoderm of adjacent gastric pouches at the base of an interradial tentacle. Fig. 47 is lower, and here the gelatinous septum completely separates the two pouches. × Zeiss H + oc. 2.

---

[1] Unless otherwise noted, the microscope was used with the draw tube not drawn out. Length of tube (dt) 137 mm.

Figs. 48 and 49 are from the same series. Fig. 48 is the second section below Fig. 47. It just clears the oesophagus. Fig. 49 is through the upper part of the stem. × Zeiss DD + oc. 2.

Fig. 50. Longitudinal section of a scyphistoma with sixteen tentacles, probably a little younger than Fig. 15. × Zeiss. DD + oc. 2, dt. 195.

Fig. 51. An obliquely transverse section of a fully developed scyphistoma, showing the relations of the septal muscles to the depressions in the circumoral disc. The mesogloea is shaded. × Zeiss B + oc. 2, dt. 160.

Fig. 52. Part of an interradial section from a scyphistoma a little older than the last. Owing to a slight obliquity of the section, the full extent of the circular sinus at the base of the tentacle is not shown. It extends to the point marked *x*. × Zeiss C + oc. 2.

PLATE 37.

Figs. 53 to 56 illustrate the development of the rhopalia.

Fig. 53. Median section of the interradial tentacle shown in Fig. 52 ; *x* marks a corresponding point in the two sections × Zeiss H + oc. 2.

Fig. 54. A radial section from the base of a rhopalial tentacle somewhat older than Fig. 23. × Zeiss H + oc. 2.

Fig. 55. Radial section of a rhopalium in the stage of Fig. 25. × Zeiss H + oc. 2.

Fig. 56. Radial section of a rhopalium in about the stage of Fig. 26. × Zeiss H + oc. 2.

Fig. 57. Radial section showing the course of a septal muscle in a strobila, at the stage of Fig. 24. × Zeiss DD + oc. 2.

Fig. 58. A similar section from a specimen a little older than Fig. 25 ; *x*, point of separation between the two discs. × Zeiss DD + oc. 2

PLATE 38.

Fig. 59. Median vertical section of a strobila in the stage of Fig. 26 ; *x*, boundary between ephyrula and basal polyp. × Zeiss B + oc. 2.

Fig. 60. Portion of section from the same specimen, showing the proboscis of the basal polyp ; *x* marks same point as in preceding. × B & L $\frac{1}{8}$ + Zeiss oc. 2, dt. 160.

Fig. 61. Median vertical section of a basal polyp, stage of Fig. 27. × Zeiss B + oc. 2.

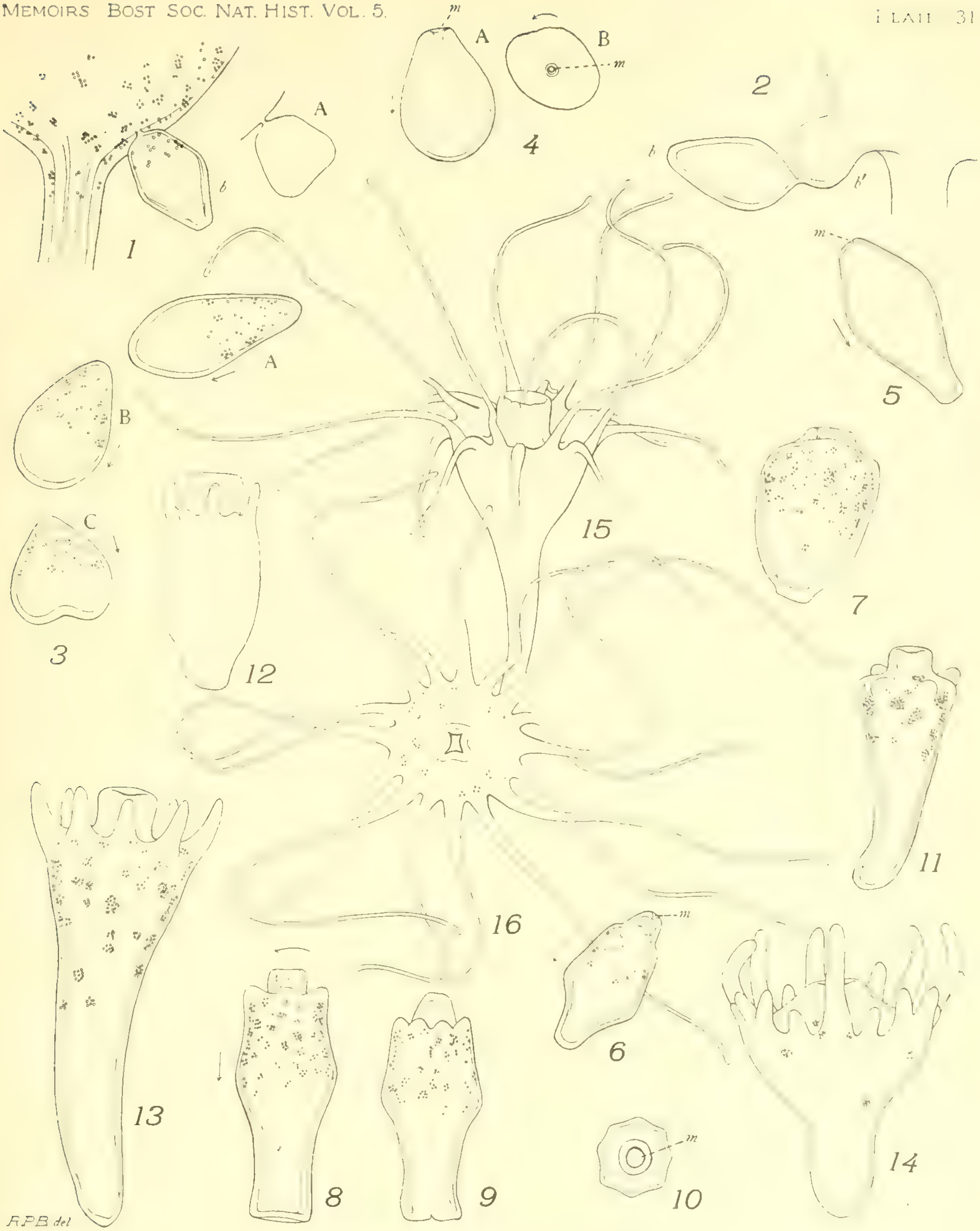
Fig. 62. Part of a section from the same specimen, showing the proboscis, p, and the vestige of the former connection with the ephyrula at *x*. × B & L $\frac{1}{8}$ + Zeiss oc. 2, dt. 160.

Fig. 63. Median vertical section of an ephyrula that has recently become free ; *x* is opposite the opening that formerly led into the cavity of the basal polyp. Cf. Fig. 29. × Zeiss DD + oc. 2.

Fig. 64. Median vertical section from a young medusa intermediate in age between Figs. 31 and 32. The section is nearly interradial in position. × Zeiss AA + oc. 2, dt. 160.

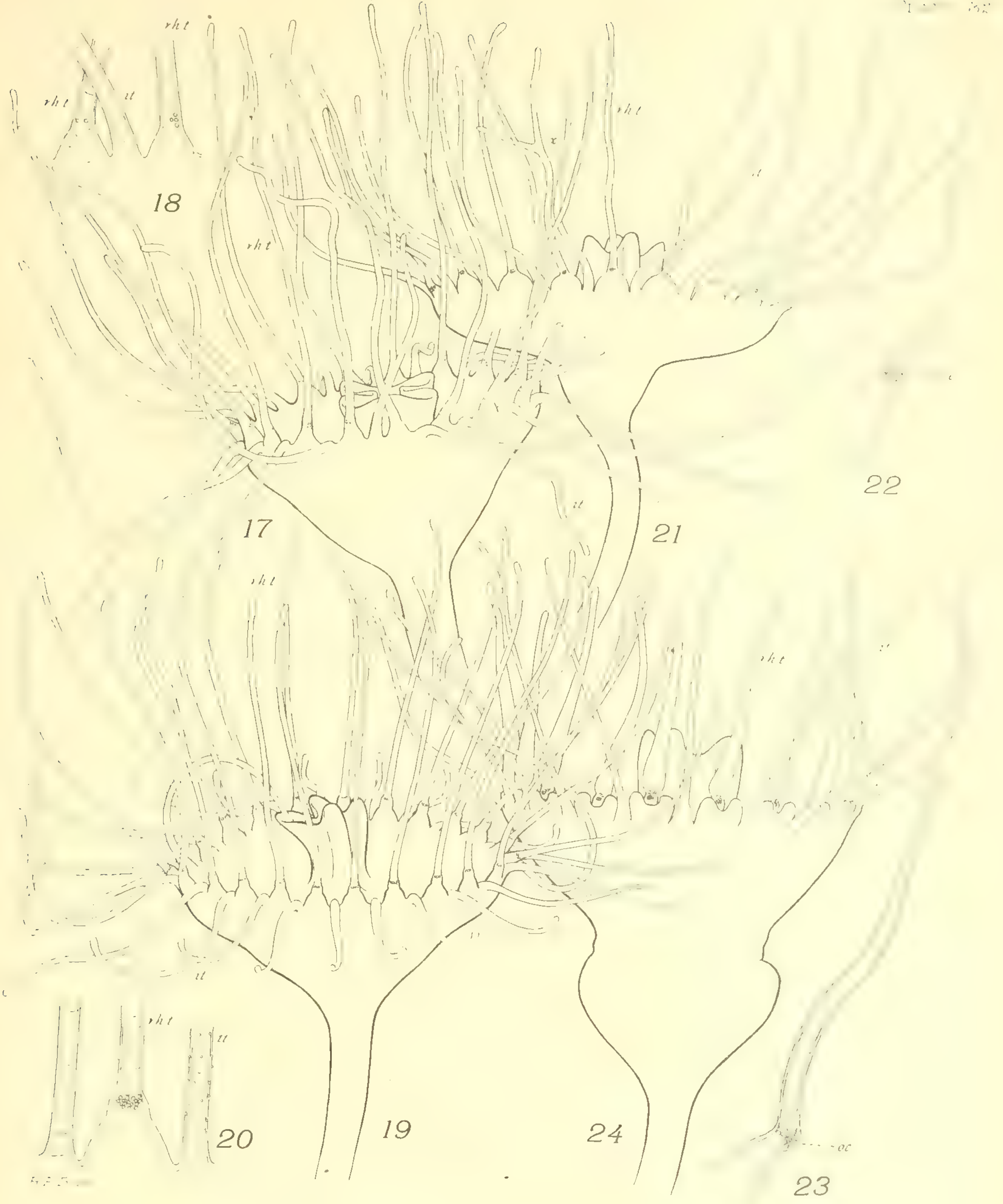
Figs. 65 and 66. Tangential sections of the same specimen, parallel to the last, nearly at right angles to an interradius. Fig. 66 is the one nearer the periphery. × Zeiss AA + oc. 2, dt. 160.

Printed, August, 1900.

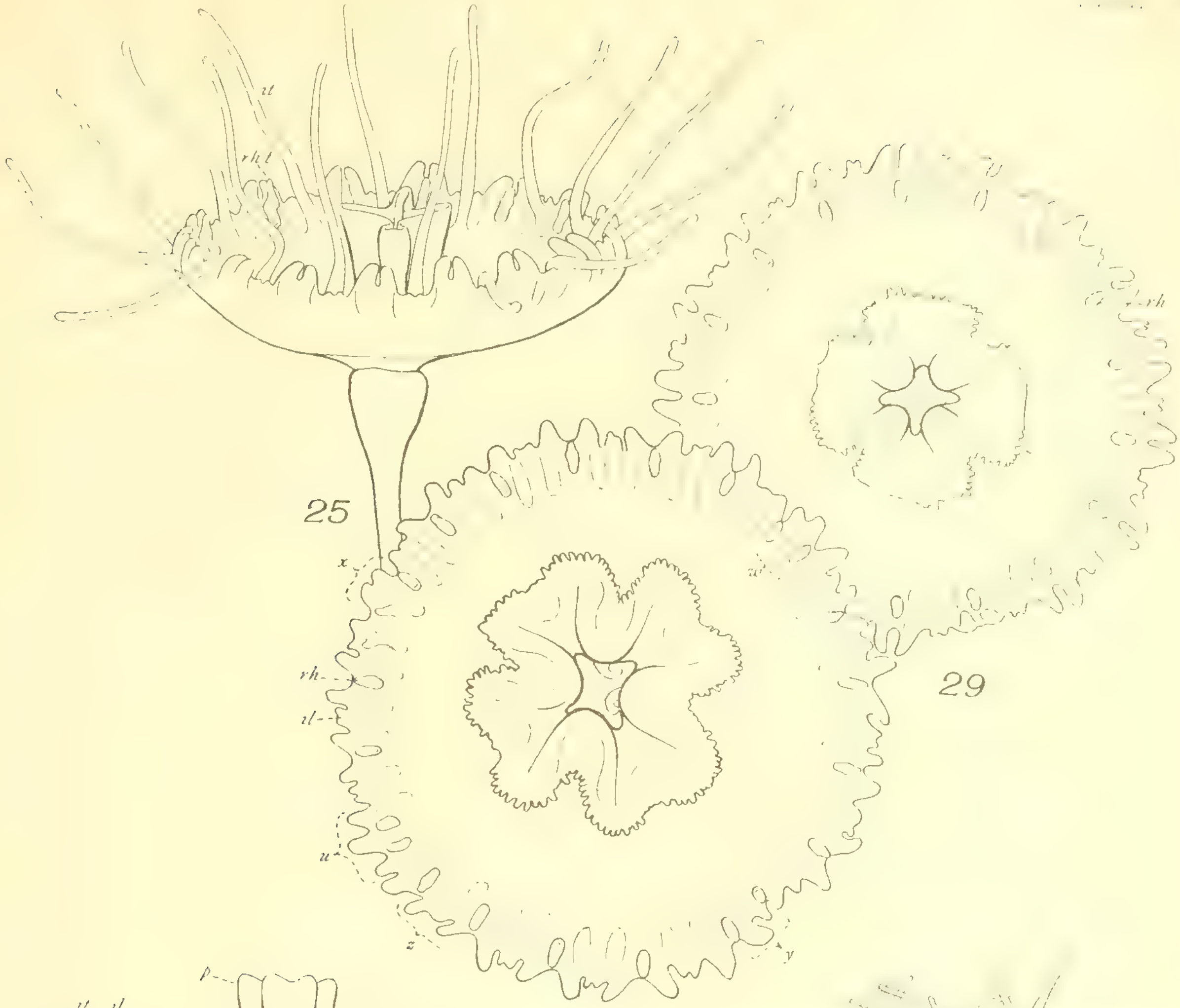


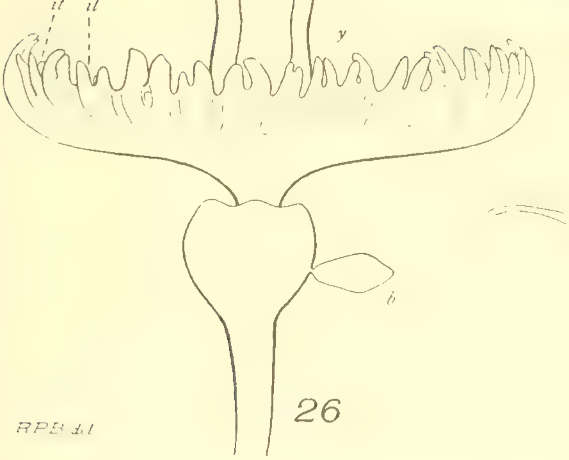
R.P.B. del.

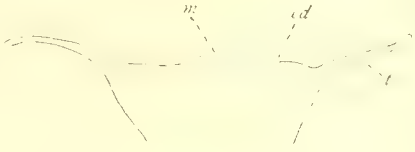
BIGELOW, CASSIOPEA XAMACHANA.

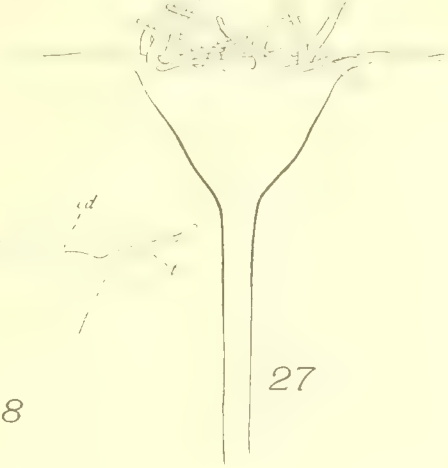


BIGELOW, CASSIOPEA XAMACHANA.

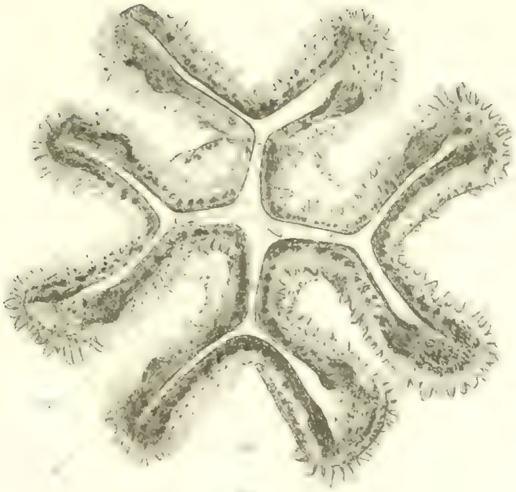


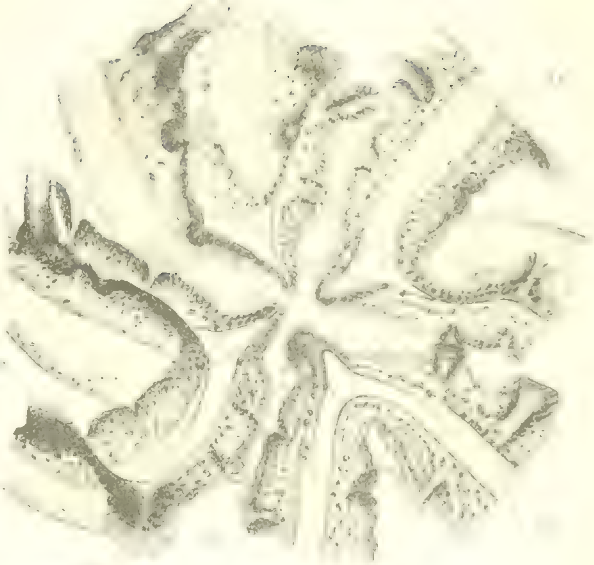


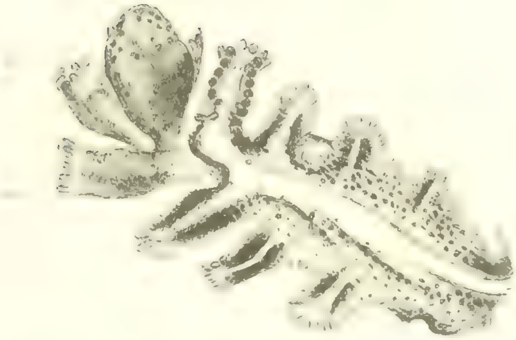




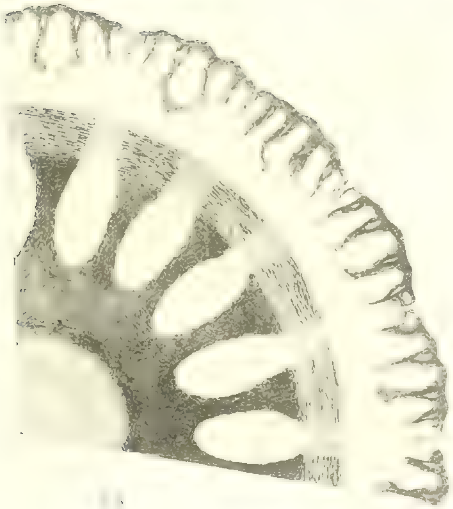
Bigelow, Cassiopea xamachana.



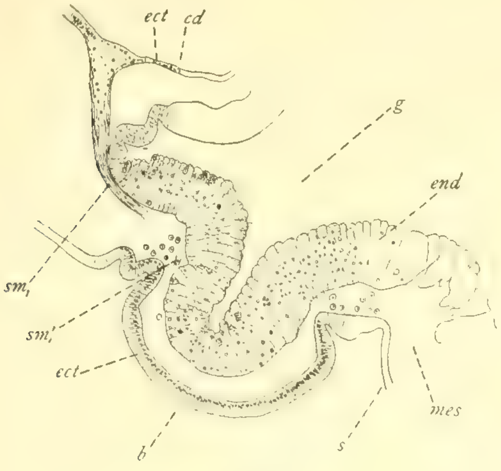




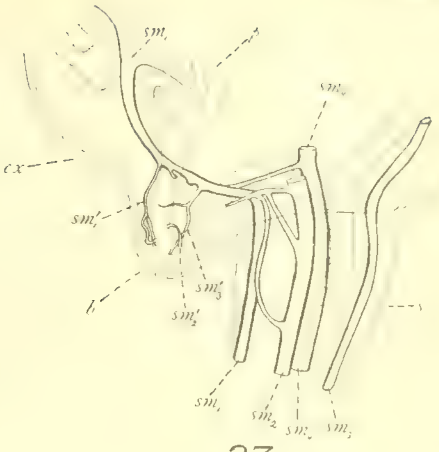
33.



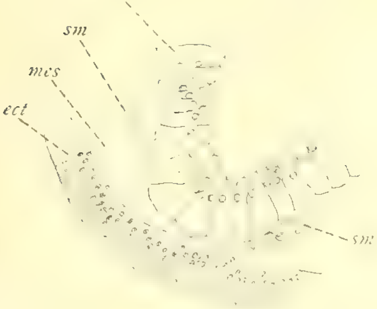
[illegible]



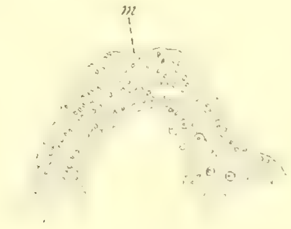
36



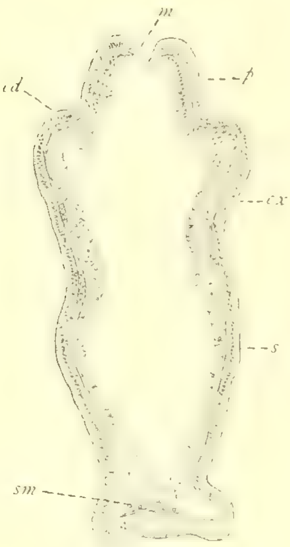
37



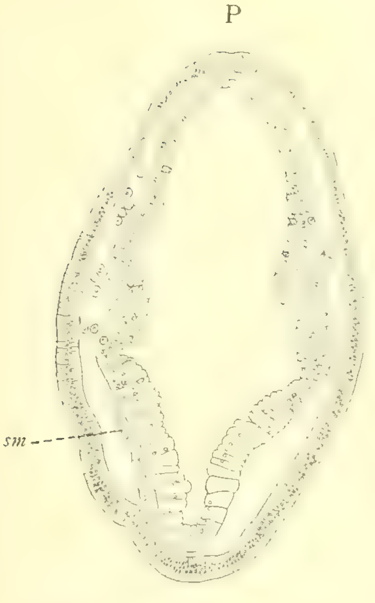
38



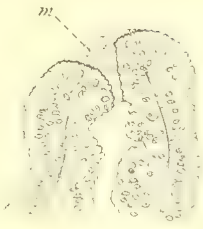
40



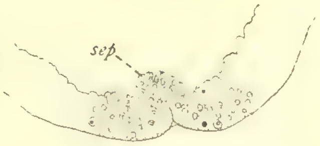
42



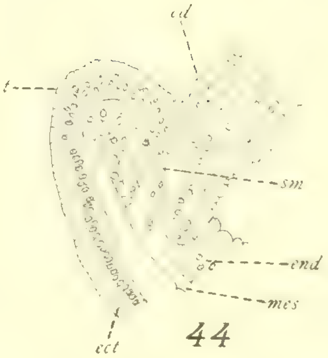
39



41



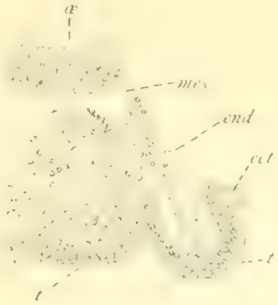
43



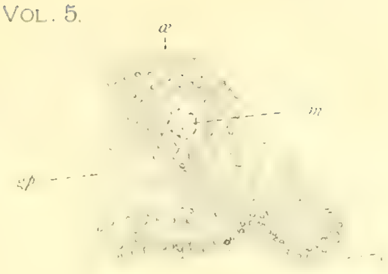
44

R.P.B. del.

BIGELOW, CASSIOPEA XAMACHANA.

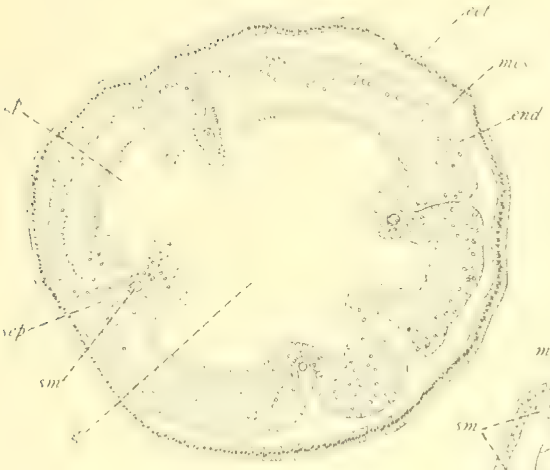


45

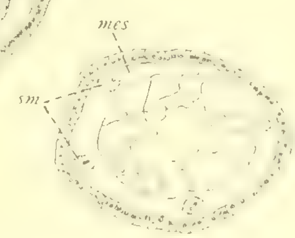


46

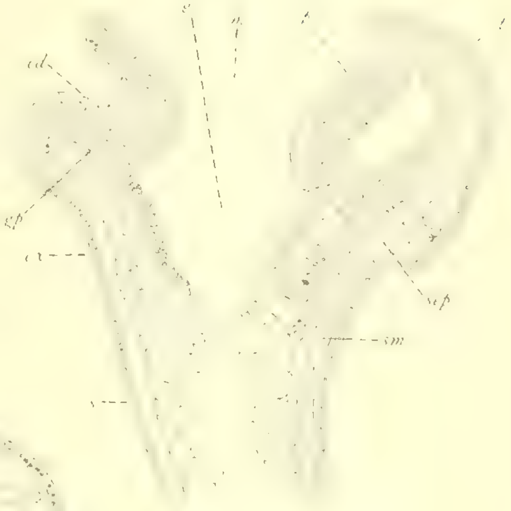
47



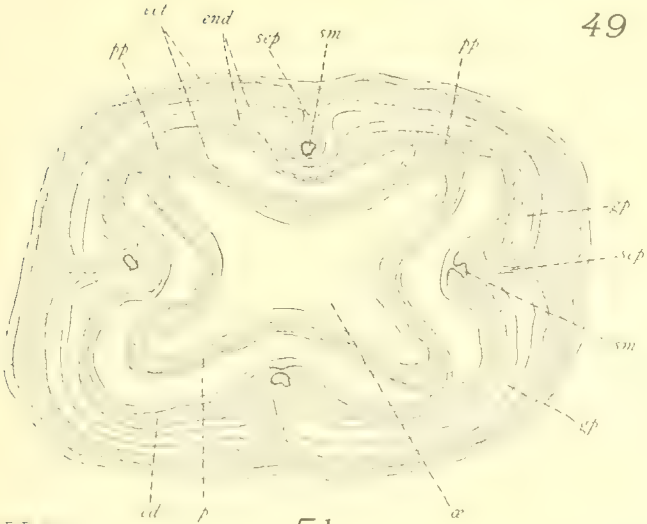
48



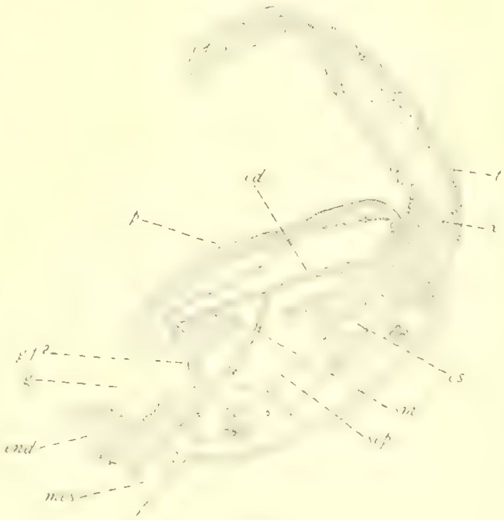
49



50



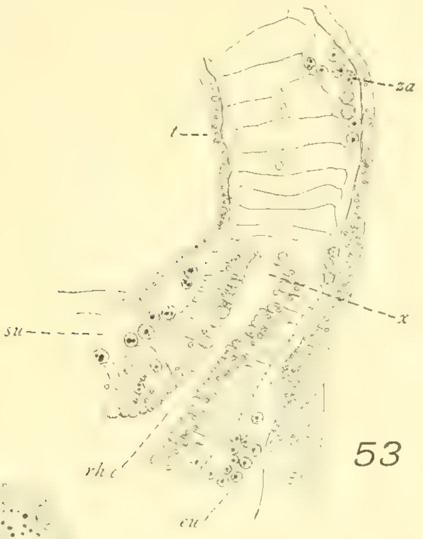
51



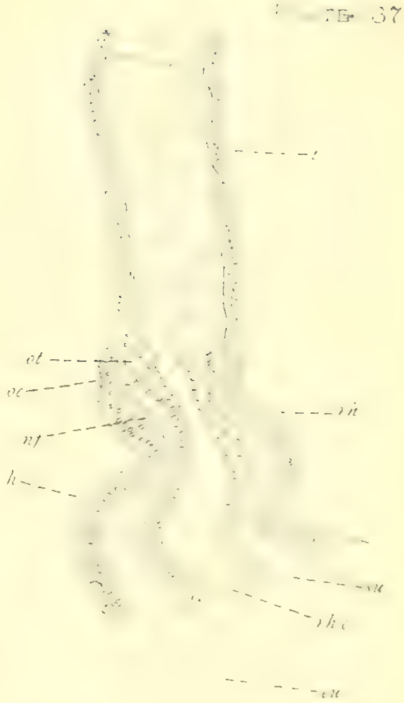
52

R F B del.

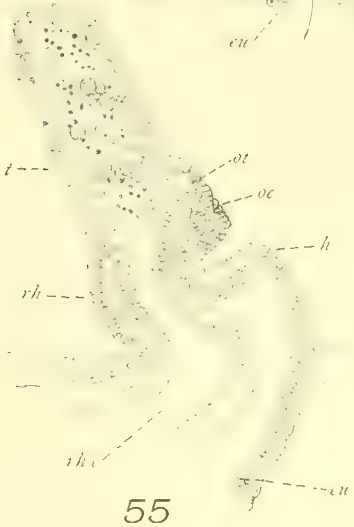
BIGELOW, CASSIOPEA XAMACHANA.



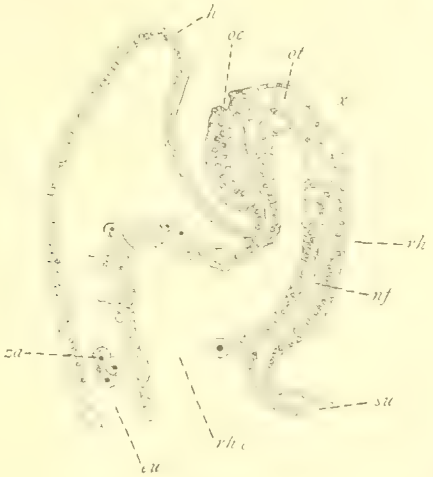
53



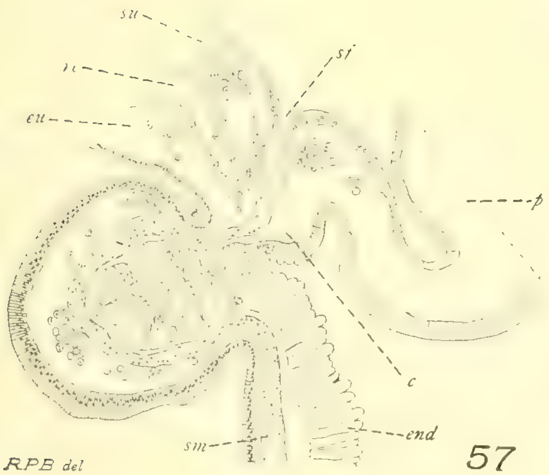
54



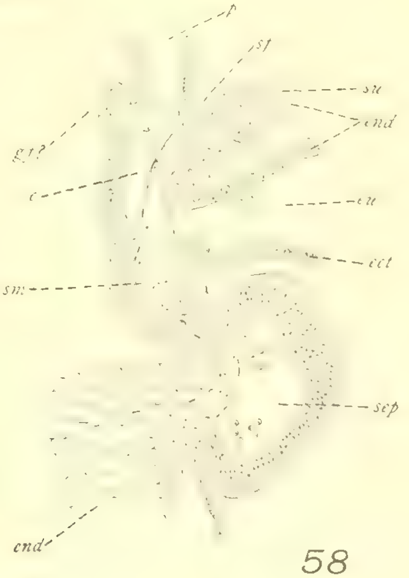
55



56



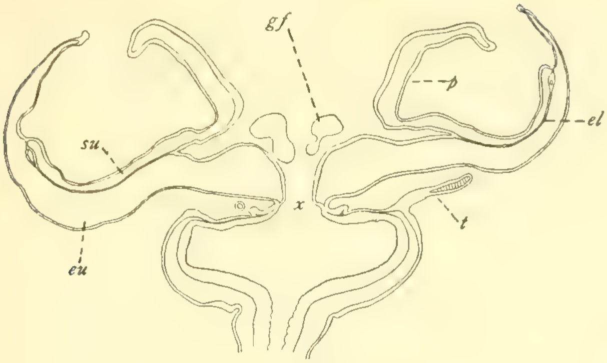
57



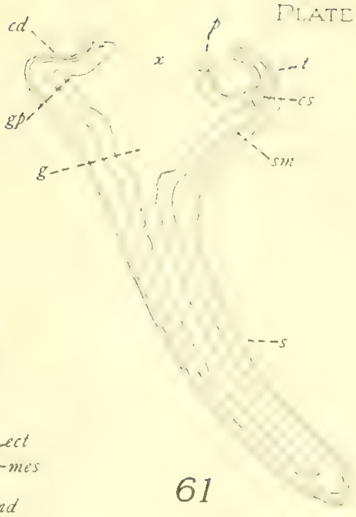
58

R.P.B. del

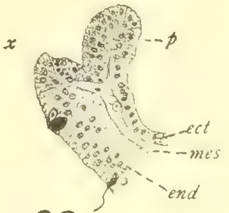
BIGELOW, CASSIOPEA XAMACHANA.



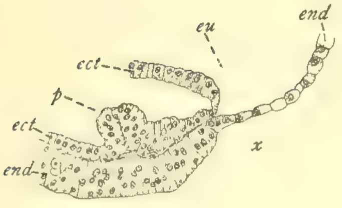
59



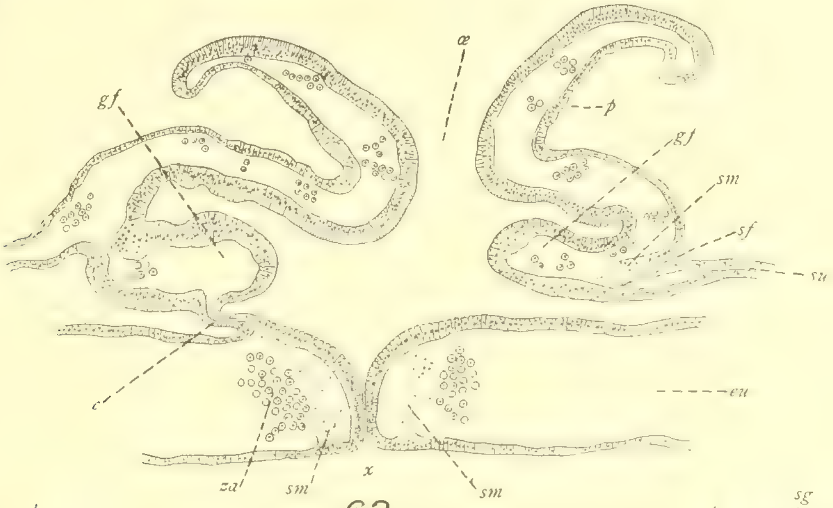
61



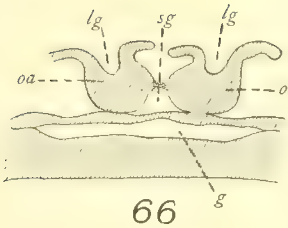
62



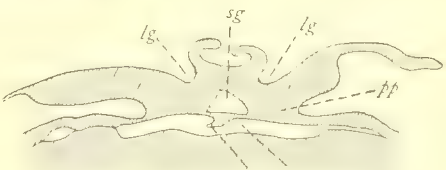
60



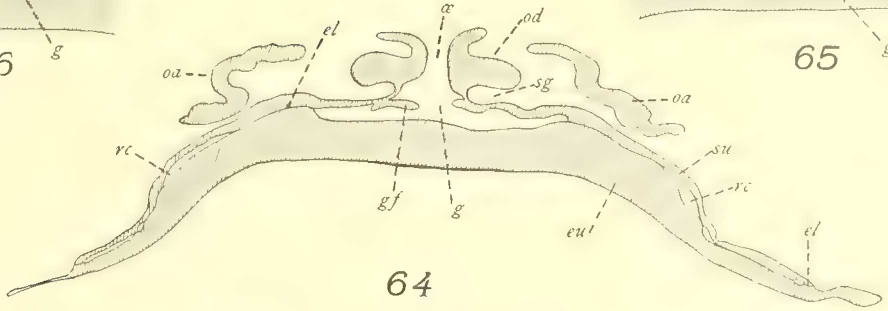
63



66



65



64

RPB del

BIGELOW, CASSIOPEA XAMACHANA.

7. DESCRIPTION OF THE HUMAN SPINES SHOWING NUMERICAL VARIATION IN THE WARREN MUSEUM OF THE HARVARD MEDICAL SCHOOL.

BY THOMAS DWIGHT.

> "Judging whether another proves his position is a widely different thing from proving your own. To establish a general law requires an extensive knowledge of the phenomena to be generalized, but to decide whether an alleged general law is established by the evidence assigned merely requires an adequate reasoning faculty. Especially is such a decision easy when the premises do not warrant the conclusion."
>
> HERBERT SPENCER.[1]

This paper is first of all a description of a collection of forty-five anomalous human spines in the Warren Museum of the Harvard Medical School, which, with one exception, were obtained by me in the dissecting-room. It represents many years' work. There are not only series representing many grades of certain peculiarities, but some specimens which I believe are unique, and others that are extremely rare. There are two spines with 26 praesacral vertebrae, of which the last is more or less sacralized on one side but certainly a lumbar. Other rare ones are mentioned later. These spines are all ligamentous preparations; so there can be no suspicion of the *inter-* or *excalation* of a vertebra by the articulator. I have carried the principle of ligamentous preparation to such an extent as to throw aside some good specimens in which the preliminary maceration had unfortunately been excessive. In two or three cases the atlas is lost, and in several the coccyx is more or less incomplete. At least once the sacrum is imperfect. Besides these spines there are several parts of the column, mostly of my collecting, which are described later. Some of the latter are mentioned by way of showing all that is in the collection, but some of them are intrinsically valuable.

The purpose of this paper is both to discuss what these spines teach concerning the significance of numerical variation of the vertebrae, which opens many important scientific questions, and to make the collection available to others.

Rosenberg's System.— The paper which, beyond all doubt, has had the most important influence on this question is that of Rosenberg (**'76**), which he has lately supplemented by another (**'99**) containing a description of a spine with two additional praesacral vertebrae and 15 ribs, of which one pair is cervical. The fundamental idea is that the vertebrae of the lumbar region are modifications of thoracic vertebrae, and that both phylogenetically and ontogenetically the ilium travels upward on the spine, so that originally the sacrum is composed of a group of vertebrae further from the head than it is later. As it advances to include vertebrae above, it releases *pari passû* others below it. If the ilium does not advance in any particular instance so far as usual, the spine is archaic; if it advances too far, the spine is of the future. In the same way the appearance of a rib on the 20th vertebra, which is particularly likely to happen when the sacrum does not include the 25th, is a return to a previous condition, while the non-appearance or imperfect development of the costal element of the 19th is a foreshadowing of what is to come. In his first paper Rosenberg put the cervical region aside; which must be borne in mind in considering his rule for the comparison of the columns of primates, namely that the last vertebra of each region at a certain stage of development is at a higher stage transformed into the first vertebra of the region below it. Evidently this cannot apply to the cervical region, for otherwise the 7th cervical would change into a first thoracic. In his last work Rosenberg has stated the matter more comprehensively. He considers (as he did before) the middle part of the thoracic region of the spine as the most primitive, and holds that the division of the column into regions (not only in man, but also in other mammals, and indeed in other vertebrates,) is the work of two chief factors which simultaneously, and to a certain extent in the same manner, exert an influence on the column in opposite directions. "These factors are both processes of transformation, of which the one, acting on the smaller proximal (i. e., cervical) division of the column, works distally; while the other, affecting the greater distal (i. e., lumbar, sacral and caudal divisions) works proximally." In other words, the cervical region on the one side and the lumbar on the other tend to absorb into themselves the thoracic vertebrae nearest to them. Such a change at either one end or the other is to be considered progressive, and a change in the opposite direction retrogressive. Rosenberg recognizes that if these two opposed factors stood to one another in a fixed relation it would be possible from the condition of one end of the thoracic region to predicate that of the other; but he admits that, so far from this being the case, the most various combinations occur. In his first paper Rosenberg enunciated the principle of concomitant variations, as for instance of the 20th vertebra frequently bearing a rib when the 25th is free, which is undoubtedly true, though not in all cases; for which it seems to me he has hardly received the credit he deserves. He never, so far as I know, has given any explanation of the cause of this phenomenon, beyond tacitly implying that when the variation was in one direction it was to be accounted for by reversion and in the other by progressive development.

---

[1] British and Foreign Medico-Chirurgical Review, Vol. XXII, Oct., 1858.

I hope to show that there is a principle to account for these changes and that, looked at from another point of view, the contradictory nature of the changes at the two ends of the thoracic region which has just been alluded to, can in many cases be explained. Certainly a theory that shall do away with such difficulties has something in its favor.

That there is much that is attractive in Rosenberg's theory is proved by the enthusiasm with which it has for the most part been received, which is natural when we consider how perfectly in many ways it fits in with the prevailing theory of evolution by gradual changes. He has the satisfaction of knowing that practically all contributions to this subject resolve themselves into a discussion of the validity of his views.

It is remarkable, however, that while Rosenberg's theory is so very generally accepted, and yet so strongly opposed by a few, his statement that the ilium enters into relation with different vertebrae during the development of the individual human foetus has never been confirmed; while it has been contradicted by Holl ('**82**), who holds that the vertebra which is the 1st sacral in the adult is such from the beginning. I myself have not had the chance to work on this embryological question, and shall therefore assume that Rosenberg's statement is justified, and limit myself to discussing whether, if so, it offers a satisfactory explanation of phenomena which it should account for.

Irregular Segmentation.—Numerical variations are explained also by *intercalation* and *excalation*, by which is meant the presence of an additional vertebra, or the absence of a normal one, between two particular vertebrae. There is some difference in the practical use of this method, some authorities meaning that in the latter case a certain vertebra is wanting and (perhaps) in the former that a certain vertebra is duplicated; while others do not go into such detail. If no particular vertebra be referred to, this theory is not very different from that of irregular segmentation. There certainly are cases that can be accounted for only by one of these methods. The best examples are found in the lower forms. The following observations by Baur ('**97**) are very convincing.

All living crocodiles have 24 praesacral vertebrae, but in a certain gavial he found 25. There is usually a sudden change in the transverse process of the 12th which is the first to have the heads of the ribs on the transverse processes only. In this gavial the change occurred on the 13th. The 9th and 10th of the normal spine have the capitellum of the rib resting on the centrum just at the level of the neuro-central suture. In this gavial there were three such vertebrae. Hence Baur concludes that there is an intercalation between the 9th and 10th. It would be better, in my opinion, to say that in the place of two vertebrae there are three, and not to attempt any more precise homology. I agree with Bateson ('**94**) that "individuality should not be attributed to a member of a series which has normally a definite number of members." Mention should here be made of the celebrated python in the Museum of the Royal College of Surgeons, discussed both by Baur ('**91**) and Bateson, in which the 166th and the 185th vertebrae are double on one side, with each two transverse processes and two ribs, while they are single on the other. What has occurred is a unilateral error of segmentation, explain it as one may.

It is self-evident that the intercalation theory, or the better one of an error of segmentation, in no way excludes Rosenberg's. The migration of a developing ilium is not in the least inconsistent with a cervical vertebra too few or too many, depending on other causes.

The Vertebra Fulcralis.—There is one important point in the discussion of the rival theories, which was raised long ago by Welcker, and which needs to be settled. According to what principle are the vertebrae of one spine to be compared with those of another? Do, for instance, the 19th and 24th vertebrae of one spine correspond to those of the same number in all others; or does the last praesacral always correspond to the last praesacral, though it be the 23d, the 24th, the 25th, or even the 26th? According to Rosenberg, and probably most biologists, the former view is to be adopted. On the other hand, in my opinion, if it can be shown that a certain vertebra has a distinct teleological significance, it is an excellent starting point. Welcker's ('**81**) idea of a *vertebra fulcralis* is a very valuable one. It is the vertebra, normally the 25th, which has the most to do in supporting the ilium, as is shown by its forming a larger part of the auricular surface than any other. According to Welcker this vertebra is always to be compared to the one having a similar function, be the number what it may. He goes even further and would have not only the whole praesacral region of one spine correspond with that of another, but he would have its component regions correspond respectively with those of other spines. While I fully adopt the former view, I am not sure that it is wise to attempt to carry it into such details. There is, however, one serious difficulty. The fact that a vertebra is the *fulcralis*, is established by its being the one that forms the largest part of the auricular surface, thus bearing more of the ilium than any other, not by its general shape. This is particularly insisted upon by Holl, who adopts the idea. It is common enough for it to be the 26th instead of the 25th, in which case there is rarely any difficulty in deciding which vertebra is the *fulcralis*. Holl declares he never has known the 24th to be the *fulcralis*, though he has seen it so sacralized that at first he was inclined to think so. In the present series there are several in which it is certain that the 24th is the *fulcralis*, but there are also some in which it is very difficult or, rather, nearly impossible to decide whether the 24th or the 25th be the *fulcralis*. Does this difficulty do away with the conception of a *vertebra fulcralis* altogether? I think not. There is nothing in the human body that is not variable, and why should we exact absolute stability from the *vertebra fulcralis?*

The Vital Principle. — My reasons for accepting the idea of the *vertebra fulcralis* are the following: Every living organism has the tendency to develop in a certain way to adapt itself to certain purposes. The fact that under changed circumstances there may be a change in development, distinctly strengthens the theory. This tendency makes for the good of the organism as a whole, which is something more than an agglomeration of fortuitous parts. Without this unifying principle the harmonious development of the various parts is incomprehensible. An essential part of the office of the spine is to form the median support of the trunk. The part above the pelvis may be considered as an apparatus with several functions. It is therefore to be taken as a whole; and the vertebra having most to do with its support can well be held homologous to the vertebra doing the same in other spines. If we admit this vitalistic conception, we can understand that there is a tendency for parts in corresponding situations to develop in a corresponding manner. Thus the penultimate lumbar vertebra (the 23d) has certain characteristics which may be found when it is the 24th.[1] Rosenberg fully recognizes this fact, but I do not see that he offers any explanation of its occurrence. The action of the vital principle is also shown in moulding parts to approach their normal conditions when some disturbing cause has interfered with the usual course of development. Instances of this will be given in the discussion of the spines.

The next question to be settled is *whether there be a precise number of human vertebrae.* It certainly is very unlikely. Fol has shown ('**85**), and his discovery has been confirmed, that at a very early time the human foetus has 38 vertebrae, some of which, however, do not persist. It would require a much larger number of observations than is likely to be made to convince one that the number 38 is absolutely constant, or that even if it be, the same number always come to maturity. In point of fact there seem to be no precise data. Steinbach ('**89**) found that the usual number of coccygeal vertebrae in the male is five, and in the female four or five. For my part I have seen so many cases in which I was unable to say with certainty whether or not certain nodules at the end of the coccyx represented vertebrae, or certain constrictions a division between two, that I admit my inability to count the coccygeal vertebrae in at least many cases. According to all analogy it is very unlikely that there should be even a fairly definite number. It is well known that variations in number of the vertebrae of the different regions increase tailwards. All the spine below the vertebrae supporting the ilium, has but a very subordinate function, and consequently is in an unstable condition. The importance of this question is on account of the objection to the theory of inter- or ex-calation or irregular segmentation, that it cannot be proved that certain elements normally on one side of the sacrum have not changed their position. This is true enough; but when the vertebrae at the borders of certain regions are characteristic ones and yet there is an abnormal number between them, the objection does not seem weighty.

---

[1] Rosenberg states that he has not himself found this condition in the case of 23 praesacrals nor, with perhaps the exception of an observation by Tenchini, found an account of it by others. There is more than one instance of at least a near approach to it in this series.

The Type.—The study of this question, absolutely independent of the point of view, brings more and more vividly before my mind the old idea of the archetype vertebra. There is no denying that the costal elements by their greater or less development are the cause of the immense majority of the variations. Originally this conception implied a plan; now it is tacitly admitted by all. The paragraph at the head of this paper is the opening one of that masterpiece of destructive criticism, Herbert Spencer's review of Owen's Archetype Skeleton. Certainly the extravagances of the dreamers who made science ridiculous were easy prey; but though it was not hard to dispose of any or all precise interpretations of the archetype skeleton, the idea of plan remains. Spencer, after demolishing Owen, tried as a substitute theory that of accumulated modifications; but it is far from satisfactory. One may think Spencer had this in mind in the first sentence of the paragraph above quoted. Indeed he points out the shortcomings of his own theory with a rare frankness: "But, it may be replied, this hypothesis does not explain all the facts. It does not tell us why a bone whose function in a given animal requires it to be solid, is formed not of a single piece, but by the coalescence of several pieces which in other creatures are separate: it does not account for the frequent manifestations of unity of plan in defiance of teleological requirements. This is quite true." The idea of plan is not easy to get rid of. The mind of man craves it. If there be nothing but absurdity in the idea of a type vertebra, how is it that the actual thing, not imaginary amplifications of it, holds its own so persistently? Let those who find a sufficient answer in "heredity" tell us how the vertebral system became so securely intrenched from the time of the first appearance of vertebrates that it has never been dislodged.

Beyond question, as was intimated above, one reason of the great success of Rosenberg's theory has been that it fitted in so perfectly with the doctrine of descent by gradual modifications. It has, unfortunately for science, become too much the custom to make everything square with this doctrine. If a certain occasional feature shows a tendency opposite to the course of phylogenesis, it is too often interpreted as necessarily a step in the direction of future modifications. This is said of undeveloped 1st, 11th and 12th ribs in man, without regard to the fact that such an abbreviated thorax could hardly be very satisfactory.

In this spirit Fürbringer ('**79**, p. 388) objects to v. Jhering's belief in inter- and excalation of vertebrae because either this theory has consequences that are in contradiction with the descent theory and *therefore* with the task of scientific morphology, or else it is a non-comprehensive theory of little value. There is at last some protest against the dogmatism that requires all phenomena to be accounted for in accordance with a certain theory. Thus Kohlbrugge ('**97**, p. 14): "I consider all so-called atavistic variations as neutral in respect to the past or future type of the race, and occasioned either by variation or by an arrest of development. This latter is caused mostly by unknown accidental disturbances manifested by irregular distribution of the developmental energy. Variations depend on the power to vary about a mean, so that they give a false suggestion of a progressive or a retrogressive developmental tendency."

I am strongly inclined to agree with Kohlbrugge on most points; but I accept evolution, with certain limitations, as the best working hypothesis, although I regard as by no means proved, nor even probable, that its course has been by a gradual succession of minute changes. Still less do I believe that the human body is, as it were, in a state of oscillation between reversive and progressive variations. Finally, I can see no contradiction between evolution on the one hand, and design and teleology on the other. While I shall draw from this series of specimens such conclusions as seem to me justified, I hope that the description will prove sufficiently accurate for those who do not agree with me to make use of them also.

Anatomical Points.—I beg leave to recall the arrangement of the *transverse processes of the lumbar region*, as they will be repeatedly referred to. Their spread increases up to the 3d. Those of the 4th or penultimate vertebra are shorter, and lighter, with a peculiar shape caused by the lower border running obliquely upward to the tip. They also spring more from the pedicle than those above them. The 5th transverse processes are thicker. They arise still more ventrally, and imply an approach to a combination of transverse process and costal element, as is seen in the young sacrum. Their length is uncertain. They are longer than those of the 4th, and may equal those of the 3d. Thus both the lowest lumbar vertebrae are characteristic.

The 3d Sacral Vertebra usually has a transverse line across the body at about its middle, indicating a change in direction of the anterior surface of the sacrum. Hermann v. Meyer believed that a line from the top of the symphysis to the middle of this vertebra is at a more constant angle to the horizon than that to the promontory. He accordingly called it the *conjugata vera.* I have taken the liberty of associating this conjugata with the transverse line which, I think, is a criterion of a normal 3d sacral. When, therefore, I say that the 3d sacral bears the *conjugata vera*, I mean that this transverse line is evident.

The *vertebra fulcralis* being accepted as a starting point, and the number of coccygeal vertebrae being disregarded as too uncertain, the following classification resting on the number of praesacrals and on the condition of the last lumbar, has been adopted.

CLASSIFICATION.

Class I.—Spines in which the number of praesacrals is normal, but in which there is an irregularity (A) at the junction of the thorax and loins, or (B) at the junction of the thorax and neck.

Class II.—Spines in which the 26th is the *fulcralis*, but in which the 25th is not quite separated from it.

Class III.—Spines in which there are more than 24 perfectly free praesacrals: (A) the extra one being thoracic, (B) the extra one being lumbar, (C) there being two extra praesacrals, one thoracic and one lumbar, the latter sacralized on one side, the 27th being the *fulcralis*.

Class IV.—Spines in which one or more praesacral vertebrae are imperfectly developed: (A) one or more vertebrae being fused, (B) the atlas being fused with the occiput, (C and D) the 24th being more or less sacralized.

Class V.—Spines in which there is a praesacral too few: (A) a vertebra being wanting in the loins, (B) in the back, (C) there being 12 pairs of ribs, the first pair being cervical and perfect on one side, the 24th being in all groups the *fulcralis*.

CATALOGUE OF THE SPINES.

Class I.

Group A. 615, G–19, 636, 567.
“ B. 1, A-30, 649, 729, 306.

Class II.

21, 561, 361, X, G–22, A–175, 2.

Class III.

Group A. 545, A–4, 764, 504, A–186, 578, 110.
“ B. 493, Y, 381.
“ C. 208, 297.

CLASS IV.

GROUP A. 264, Z.
" B. 24.
" C. H–3.
" D. 349, 492, 257, A-219, A–7, 141.

CLASS V.

GROUP A. D-7, 85, 377.
" B. 350, 478.
" C. 267, 202.

As the above classification necessarily scatters peculiarities (cervical ribs for instance) which are generally kept together, the following table of the spines and incomplete specimens presenting certain peculiarities has been prepared. In some cases of doubtful interpretation the same specimen figures in more than one category. This also occurs when one specimen presents more than one of these peculiarities.

CERVICAL RIBS: 4, A-30, 649, 729, 306, H–3 (?), 349, 492, 267, 202. Incomplete specimens: 725–2, 9379–37.

RUDIMENTARY FIRST THORACIC RIB: G-22, (not rudimentary but small) A–4, H–3 (?). Incomplete specimens: 140, 572.

BICIPITAL AND TRICIPITAL RIBS: 649, 208. Incomplete specimen: C 4.

FUSION OF ATLAS AND OCCIPUT: 561, 24, D–7 (probably pathological). Incomplete specimens: 7737–3, 9638, 9639, 8590, 132 (probably pathological).

FUSION OF ATLAS AND AXIS: H–3.

FUSION OF AXIS AND THIRD VERTEBRA: 297 (?), 264. Incomplete specimens: 4767, 1392.

SUPPRESSION OF A CERVICAL VERTEBRA: H–3, 202 (?).

EXTRA HALF VERTEBRA: 9395–3.

The following are among the most remarkable spines: 208, 297, two additional praesacrals with the last one sacralized on one side; 264, fusion of axis and 3d; Z, fusion of and arrested development of several lumbar vertebrae; H–3, fusion of atlas and axis, suppression of a cervical vertebra, an additional lumbar, sacralized on one side; 267, unique anomaly of atlas, cervical rib on one side reaching sternum, suppression of a thoracic vertebra; 202, cervical rib to manubrium on one side, with the next rib ending in place of normal 2d, with no contact between the cartilages, suppression of a thoracic (or cervical) vertebra.

CLASS I.

This class comprises the spines in which there is the normal number of praesacral vertebrae, but in which there is some irregularity of the costal element at the junction of the thoracic region with the loins or with the neck. The former cases are in Group A, the latter in B.

The following spines are in Class I. Group A: 615, G–19, 636, 567; Group B: 1, A–30, 649, 729, 306.

Group A.

The peculiarities of this group are so common that it might have been enlarged indefinitely. Either the costal element of the last thoracic vertebra (19th) is too small, or that of the next below it is too large.

615. Cat. 9379–4.[1]

Female, white, aet. 63. Vertebral formula: C. 7, T. 12, L. 5, S. 5, (C. 4 ?).

This is the slightest possible deviation from the norm. The only peculiarity is that the last ribs are very small, and, though doubtless originally distinct, are now fused with the 19th vertebra. The length of the right one is 3.5 cm., and of the left 2.6 cm. The spread of the lumbar transverse processes is normal, increasing to the 3d. The 4th sacral is a penultimate. The change of the articular processes between back and loins occurs normally. There is nothing irregular or transitional in the sacrum except that only two vertebrae articulate with the ilium. The *conjugata vera* is at the 3d sacral, near the top. The pieces of the coccyx are fused, and their number is uncertain.

---

[1] The first number is that used in the dissecting room, the latter the one put on when the specimen is entered in the catalogue of the Museum. I always refer to a specimen under the former number, as it is the one under which I have studied it. As both numbers are kept on the specimen card there is no difficulty in using either.

G–19. Cat. 9379–5.

Female, white. C. 7. T. 12. L. 5. (S. 5. C. 5 ?).

The 12th pair of ribs are very small. The left one has a minute, but distinct head in a socket, while the right one is even more rudimentary, being incorporated with other parts so as to suggest a transverse process. The left one measures 2 cm.: the right one is 3 mm. shorter. Seen from the front, the right one continues the line of the heads of the ribs; seen from behind, it is distinctly a transverse process. The 19th vertebra as a whole is thoracic rather than lumbar, the spinous process being thoracic and the change of the articular processes occurring below it. The spread of the lumbar transverse processes is not characteristic, as it is about equal in the lower four, but those of the 4th lumbar have the penultimate outline. There seem to be 9 or 10 sacral and coccygeal vertebrae. The 5th sacral looks very much like a coccygeal fused with the sacrum. Little if any of the 3d sacral touches the ilia, but it has the *conjugata vera*. Below what I have called the sacrum there are 4 or 5 coccygeals fused together. The 11th pair of ribs measures, on each, side, 15 cm. along the concavity. This increase of length is common when the last pair is rudimentary or with lumbar characteristics. Although the spine was not measured fresh, it is evident to the eye that proportion requires that the 19th vertebra be considered thoracic.

In this spine the tendency in the 19th to assume a lumbar character has gone further than in the preceding, one sign of which is the disturbance of the customary rule of development of the lumbar transverse processes.

(In the two preceding cases there is a tendency for the 19th vertebra to assume lumbar characteristics; in the two following it is for the 20th to assume thoracic ones.)

636. Cat. 9379–36.

Male, white, aet. 28. C. 7, T. 12 or 13, L. 5 or 4, S. and C. 10.

The costal elements of the 1st lumbar are separate. The left one seems like a transverse process that has not fused with the body, but the right one has both the shape and size of a rib. There is a distinct head in a socket. The length of the right one is 4.3 cm., and of the left 2.5 cm. The lumbar transverse processes are very peculiar, those of the 21st and 22d being uncommonly strong, and those of the last two uncommonly small. The last is very ill developed, suggesting that of a penultimate. On the right they increase in length to that of the 23d, on the left to that of the 22d. That is to say, if we consider the 20th a lumbar vertebra on the left and a thoracic on the right, the 3d lumbar on each side has the greatest spread. The change of the articular processes is normal.

i. e., below the 19th. The sacrum is remarkable in two ways: the lateral masses of the 1st piece rise very high, as though trying to join the last lumbar, and, while a small part of the 3d articulates with the ilium on the right, none of it does on the left. This accords with the downward movement of the thorax and loins on the right. On the other hand the sacrum is normal in having a very strong promontory and the *conjugata vera* on the 3d. All the sacral and coccygeal vertebrae are fused. There are probably five of the latter.

The measurements and proportions from the fresh spine are as follows.

	Length of 636.	Average length, male.	Proportions of 636.	Average proportions.
Neck	12.7 cm.	13.3cm.	20.5%	21.5 %
Back	29.3	28.7	47.3	46.3
Loins	20.0	19.9	32.2	32.2
Total	62.0	61.9	100.0	100.0

It is clear that the 20th vertebra, as far as proportions go, must be called lumbar in spite of its aping the thoracic region on the right. Very interesting are the concomitant changes in the spread of the lumbar transverse processes; but what is peculiar and not so easy to account for is the apparent effort of the sacrum to encroach on the loins, and the fact that the 24th is somewhat of a penultimate.

567. Cat. 9379–6.

Male, white, aet. 59. C. 7, T. 13, L. 4, S. 6, C. 4.

In this case the process has gone further and there are 13 pairs of ribs. The 13th ribs have heads, that of the left one being ill marked. The right rib is 4.7 cm. long, the left 4.3 cm. Both are evidently more in series with the ribs above them than with the transverse processes. The change of the articular processes occurs below the 20th vertebra. Its spinous process, though intermediate, is lumbar rather than thoracic. The external tubercle, especially on the right, is uncommonly developed in this vertebra. The spread of the lumbar transverse processes increases to the 23d. The lateral masses of the sacrum show a tendency (that did not appear in the preceding spine) to mark off transverse processes. The 6th piece of the sacrum strongly suggests a fused coccyx. The 3d sacral has a considerable surface articulating with the ilium. The *conjugata vera* is probably at the 4th sacral. It seems as though the thorax were encroaching on the loins; nevertheless the proportions clearly require the 20th vertebra to be considered thoracic in spite of its lumbar peculiarities.

These four cases illustrate what may be called the instability of the region at the junction of the back and the loins. It is curious to see how similar the conditions of the last costal elements are in G 19 and 636, though occurring in the former at the 19th, and in the latter at the 20th vertebra.

Group B.

This group, like the preceding, has the normal number of praesacral vertebrae, but there is some irregularity in the costal element at the junction of the neck and back. This might consist either in cervical ribs or in a want of development of the 1st thoracic rib. In point of fact the only complete spine with the latter anomaly has to be put in another group. The same is true of several cases of cervical ribs.

1. Cat. 9379-14.

Adult. C. 7. T. 12. L. 5. S. 5. C. imperfect.

A pair of small cervical ribs, the right one fused, the left free. Length of right rib along anterior curve 2.7 cm. It ends free in a sharp point about 1 cm. beyond the transverse process. The left one is longer (4. cm.) and much more evidently a rib, with head, neck, and tubercle. All these parts are minute. It also ends free in a sharp point directed forward. On the left the so-called costal element of the 7th vertebra is present behind the rib, with the usual transverse foramen.[1] The 1st thoracic ribs are not quite typical, the left one, especially, being uncommonly long and narrow. Though inserted as a 1st rib, it resembles a 2d. The 11th ribs measure 17.2 cm. on the right, and 16.7 cm. on the left. The 12th pair is rather small: 7.8 cm. on the right, and 7. cm. on the left. The change in the articular process occurs normally. The transverse process of the 4th lumbar is that of a penultimate on the right, but not on the left.

This spine is in most respects, and as a whole, very normal. There is, however, a greater peculiarity than the presence of cervical ribs. It is the concomitant change in the 1st thoracic ribs and the lack of development of the 12th pair, hinting at a tendency of the thorax to move upward.

A-30. Cat. 9379-31.

Black, male, aet. 22. C. 7, T. 12, L. 5, S. 5, (C. 4 ?).

There is a small cervical rib on the left, consisting of a minute head, tubercle, neck and shaft, ending free in a point. The length, following the curve, is 2.6 cm. The right costal element of the same vertebra is wanting, probably lost, for there is the faintest

[1] For the explanation of this condition *vide* Leboucq, ('96, 98).

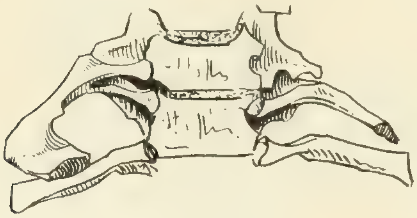
possible suggestion of a facet on the body of the vertebra, and a somewhat clearer one for the tubercle. The length of the last ribs, following the curve, is 8 cm. for the right one and 5.4 cm. for the left. The spread of the lumbar transverse processes is not typical, and the lateral masses of the sacrum rise considerably. The proportions, measured on the fresh spine, are very correct. There is little to note in addition to the above.

It is probable that the lost right cervical rib was the smaller. If that be so, it is interesting to note that the smaller last ribs are on the same side as the larger cervical one, indicating a tendency of the left side of the thorax to rise. This would not be mentioned, were it not in accord with several other undoubted cases of the same phenomenon.

649. Cat. 9379–29.

Female, white. C. 7, T. 12, L. 5, S. 5, (C. ?).

This is a case of a *bicipital* rib on the right, formed by a cervical rib fusing with the 1st thoracic beyond the tubercle. The head, neck and tubercle of the cervical rib are nearly as large as those of the 1st thoracic. The right transverse process of the 7th cervical vertebra is much larger than the left one. The transverse process of the 1st thoracic runs sharply upward to meet it, leaving a large gap on the right at the back, between the 1st and 2d thoracic ribs. The spinous process is peculiar, being compressed laterally so that the end is long vertically, and suggests two tips one above the other. The lower part of the spine, without showing any great irregularity, is not typical. The last ribs are small, the right one measuring in a straight line 4.4 cm., and the left one 4. cm. It is worth noting that the one on the same side as the cervical rib is the longer; which is an exception to the concomitant changes so often observed. The change of the articular processes is at the normal place, but rather transitional on the right. The spread of the lumbar transverse processes is not quite characteristic. The 5th sacral is imperfect on the right side, there being only three sacral foramina. The coccyx seems short, but the number of pieces is uncertain. The cervical region is relatively short, although the 7th vertebra is retained in it. The following measurements are from the fresh spine.



649.

	Length of 649.	Average length, female.	Proportions of 649.	Average proportions.
Neck	11.8	12.1	20.3%	21.2%
Back	26.9	26.5	46.4	46.1
Loins	19.3	18.7	33.2	32.7
Total	58.0 cm.	57.3 cm	99.9	100.0

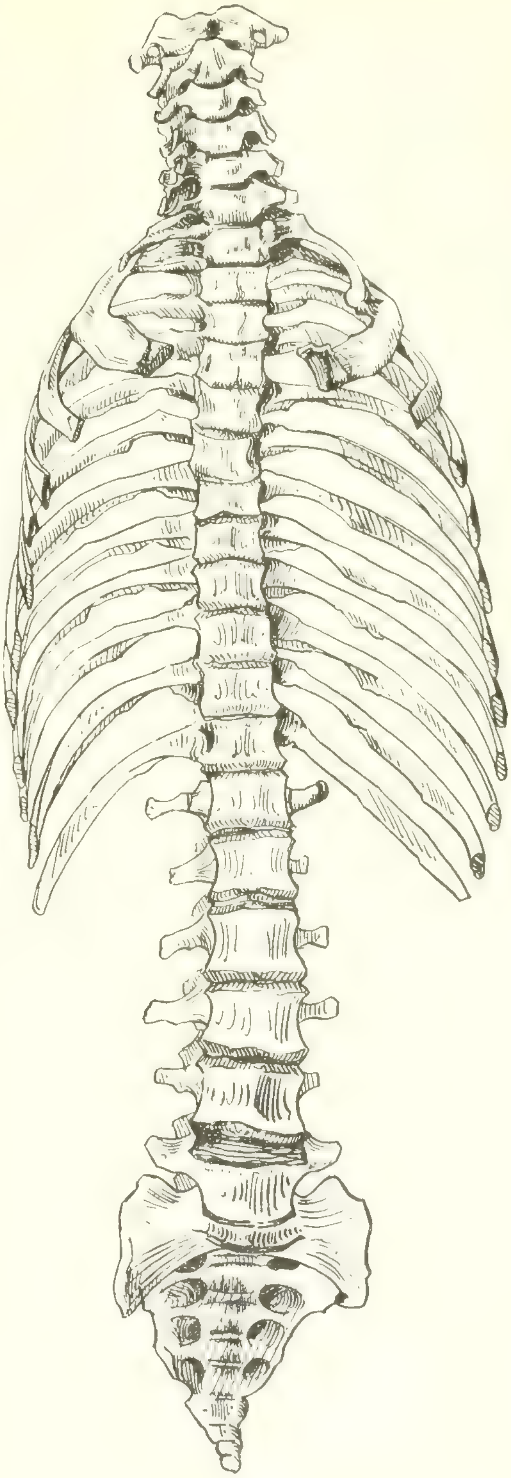
(The two following cases of cervical ribs are much alike. The last ribs, on the 19th vertebra, though separate, much resemble transverse processes. The thorax seems, therefore, to have moved upwards.)

729. Cat. 9379–32.

Female, white, aet. 26. Vertebral formula normal. (The sacrum has 5, and the coccyx 4.)

The right cervical rib is small, consisting of a head, neck, tubercle and a minute shaft ending free in a point. The length, following the curve, is 3.2 cm. The left cervical rib is 6.2 cm. long and altogether larger. It ends free in a knob to which shreds of muscle were attached. Just behind this is a smooth groove, no doubt for the subclavian artery. It was connected to the first thoracic rib by muscular fibres, having the direction of the external intercostal. There was no internal layer. The pleural cavity extended up to the cervical rib. The 1st thoracic ribs, especially the left, encroach somewhat on the body of the 7th vertebra. The right one is tolerably normal, with two ill-marked grooves. The left one is longer, narrower, and a good deal like a 2d rib. It has a groove, presumably for the vein, just in front of the end of the cervical rib. Seen from behind, the transverse processes of the 7th cervical are abnormally expanded. The proportions of the body of this vertebra resemble those of a 1st thoracic, and the latter does not have the usual slight elevation of its superior lateral borders.

The costal elements of the 19th vertebra resemble closely lumbar transverse processes which have been cut through some 5 mm. from the base, so that the greater part is movable.



729

The free portion is 2.3 cm. long on the right, and, 2.2 cm. on the left. Their spread is greater than that of the transverse processes of the 1st lumbar. The pleura lined the right one, but on the left this could not be determined. The change in the articular processes is one place too high: between the 18th and 19th vertebrae. The greatest spread in the lumbar region is at the 3d, but the 2d almost equals it. The *ligamenta arcuata externa* ended at the tips of the 11th ribs. Some few facts concerning the nerves could be gained. Apparently the formation of the brachial plexus (as far as the entering nerves were concerned) was normal. The only nerves in the lumbar plexus that could be identified with absolute certainty on both sides were the anterior crural and the obturator, which were formed by the 2d and 3d lumbar nerves. The right lumbo-sacral cord seemed to come from the 4th nerve rather than from the 5th, which latter joined the 1st sacral. On the left nothing satisfactory could be made out.

From all this it seems that there was a tendency for the thorax to ascend, and for the lumbar and sacral plexuses to ascend with it. The position of the external arcuate ligament implies a similar tendency. In spite of its lumbar peculiarities the 19th vertebra has to be reckoned as thoracic to maintain the proportions as much as may be.

	Length of 729.	Average length, female.	Proportions.	Average proportions.
Neck	12.3	12.1	21.4%	21.2%
Back	26.1	26.5	45.5	46.1
Loins	18.0	18.7	33.1	32.7
Total	56.4	57.3	100.0	100.0

306. Cat. 9379 — 29.[1]

Black, male.

This spine is very like the last one. There is the usual number of vertebrae, the sacrum consisting of five, and the coccyx of four. Both these regions are unusually small. The cervical ribs are much smaller than those of the last case. The right one, measured along the concavity, is 3.6 cm. The left is rather shorter, but an injury prevents accurate measurement. Each ends free; muscular fibres, having the direction of the external intercostal, running from them to the first ribs. The subclavian artery crossed just beyond the cervical rib, resting on the front border of the muscle. Pretty nearly the same thing may be said of the bodies of the 7th cervical and of the 1st thoracic vertebra as in the last case; but the first thoracic ribs do not touch the body of the former. The 12th thoracic ribs also resemble transverse processes in much the same way. They apparently once had heads, but anchylosis made such progress that they look like transverse processes. The transverse processes of the 17th vertebra (10th thoracic) have no articular surfaces, and those of the 18th are broken up like those of the ordinary 19th. The costal element of the 19th does not extend so far outwards as the transverse process of the 1st lumbar. The change in the articular processes is between the 18th and the 19th, one place higher than usual. The greatest spread in the loins is at the 3d. The measurements on the fresh spine were as follows, whence it appears that the loins are exceptionally long even if (as is clearly right) the 19th vertebra be reckoned as thoracic.

---

[1] Dwight '87, p. 548, where it is marked "case [illegible]" instead of "case 2".

	Length of 306.	Average length, male	Proportions	Average proportions
Neck	12.2 cm.	13.3	20.8%	21.5%
Back	25.3	28.7	43.2	46.3
Loins	21.1	19.9	36.0	32.2
Total	58.6	61.9	100.0	100.0

This is a clear case of over-development of the costal elements of the 7th vertebra, and concomitant under-development of those of the 19th, the thorax apparently moving up.

The spines of Group B, excepting the one with the bicipital rib, show more or less clearly what with others I am inclined to call a forward or upward moving of the thorax, shown by the over-development of the costal element of the last cervical vertebra, often by more or less modification of the 1st thoracic rib, and by the under-development of the last pair. These concomitant changes may occur on both sides or on one. This moving of the thorax forward or backward, either as a whole or on one side only, is a phenomenon that is perfectly well known. How it is to be accounted for on the theory that such changes are either regressive or progressive is beyond me. Bateson objects, not without reason, to this phraseology; and instead of speaking of the thorax moving forward (which it does not actually do), he would call it *backward homoeosis*, because the last elements of the cervical and thoracic regions tend to assume the features of the regions behind them. Without disputing the justice of his criticism, I feel that the expression originally employed of "the thorax moving forward" more readily supplies a mental image, and saves us from a new word.

It is worth noting that in every spine of Class I the proportions have required the 19th and 20th vertebrae to be reckoned respectively as thoracic and lumbar, whatever may have been their peculiarities.

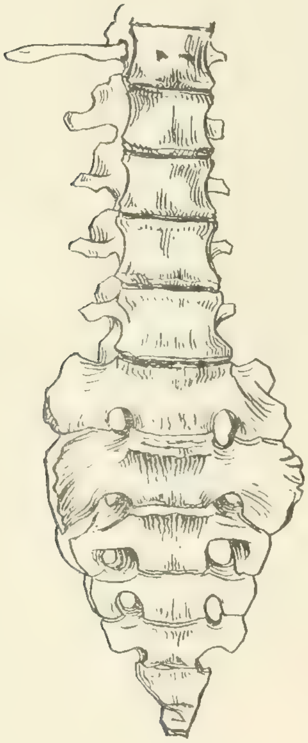
CLASS II.

(21, 561, 361, X, G–22, A–175, 2.)

This class includes spines in which there is an approach, more or less near, to 25 perfect praesacral vertebrae. In the first the 25th vertebra is almost a sacral one, in the last it is almost a pure lumbar. They are arranged to mark the steps of this progression as regularly as possible. In every one of this class the 26th is the *vertebra fulcralis*, i. e., the one having the largest surface articulating with the ilium. Also in every case there is more or less of a disc between the 25th and the 26th. As the degree of sacralization of the 25th has been made the basis of arrangement of this class, it has been necessary to disregard the number of ribs, and even the synostosis of atlas and occiput.

21. Cat. 9379–7.

Female, white, aet. 10. C. 7, T. 13, L. 5, S. 4, (C. 4?).



21.

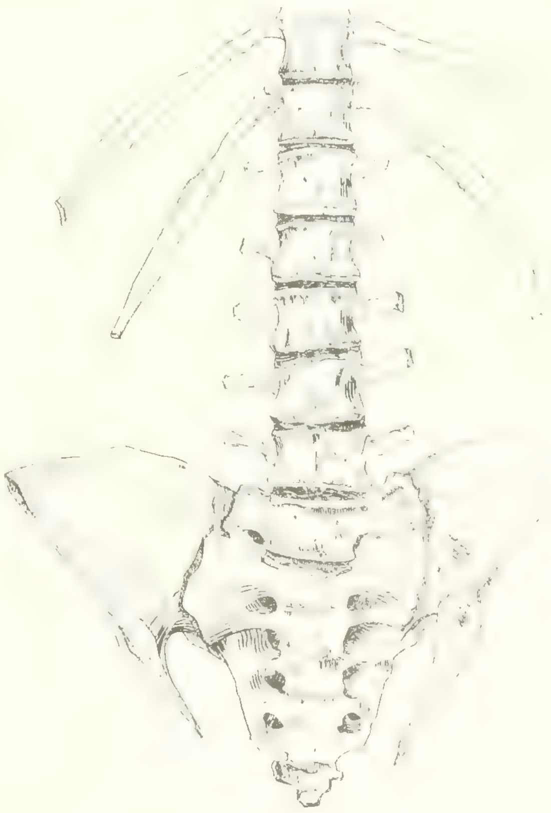
There is some difficulty in deciding the limits of this sacrum; but in view of the facts that the 26th is clearly the *fulcralis*, and that the 20th is a thoracic at least on one side, I have put the 25th in the lumbar region though it superficially resembles a sacral vertebra very strongly, and there are only 4 sacrals below it. The coccyx is hard to count, probably containing 4 pieces.

There is nothing worthy of note above the 20th vertebra, which has a distinct rib on the right, 3.7 cm. long, with a head, and clearly in line with the others. On the left the costal element has been lost in the preparation. It was almost wholly cartilaginous, from 1 to 2 cm. long. No certain facet for a head can be found. The change in the articular processes is ill marked, apparently occurring, on the right, below the 19th, and on the left, a vertebra lower. The spread of the transverse processes of the loins is about the same (excepting the 25th) and is a little greater in the first. The 25th has an ill-marked promontory below it. It forms a part of the convexity of the loins, and there is the slightest suspicion of a promontory above it. This want of a very definite promontory is characteristic of the sacrum of childhood. The lateral masses of the 25th are very sacral in character, touching those of the vertebra below, though of course not fused at this early age. They form a portion of the auricular surface, though less than half as much as those of the 26th, which is certainly the *fulcralis*. It is probable that the auricular surface extends to the 2d sacral. The disc below the 25th in the dried spine is almost as thick as the one above it.

561. Cat. 9379–15.

Male, white, aet. 28. C. 7, T. 13, L. 5, S. 5, C. imperfect.

This spine shows a tendency to shorten at the upper end, by the atlas fusing with the occiput, and to lengthen below, the 25th vertebra not being a true sacral. There is also some confusion at the junction of the back and loins. The fusion of the atlas with the occiput is pretty nearly complete, but the parts of the former are all distinct. On the right the arch tends to lose its individuality, while on the left there is a space between it and the skull. The neck and back present nothing peculiar above the 12th ribs, which are very long: 15.3 cm. on the right, 15. cm. on the left, following the concavity. The heads are placed higher than normal, encroaching largely on the cartilage above the vertebra. The 13th pair of costal elements, though movable, resemble very closely lumbar transverse processes, especially the left one, the right being more slender and rib-like. Each measures 2.5 cm. The change of the articular processes is below the 20th vertebra. The first lumbar transverse processes are small, after which their spread is about the same. The 5th lumbar is transitional and unsymmetrical. The body is deeper on the left, and the lateral mass of that side the larger, with a rudiment of a transverse process. It is bound close to the ilium and probably forms a small part of the joint. On the right it does not quite touch the ilium. The 3d piece of the sacrum has no share in the auricular surface of the left, and but a very slight one on the right. It is the seat of the *conjugata*



561.

vera. It is much to be regretted that the first ribs had been cut a little beyond the tubercles, and that the spine was not measured when fresh. It is to be noted that on the left (the side in which the atlas is most free) the 25th vertebra is more sacralized, and that on the right (where the arch of the atlas is nearly absorbed into the occiput) the 25th is more nearly a normal last lumbar, thus showing an effort to keep the normal number of praesacral vertebrae on each side. Further on the left the costal element of the 20th vertebra is more like a lumbar transverse process, while on the right it is more like a rib, thus showing an effort to keep the normal number of five lumbar vertebrae. The great length of the penultimate ribs is characteristic of a spine with aborted last ones.

361. Cat. 9379–17.

Female, white. C. 7, T. 12 (13), L. 6 (5), S. 5 (?), C. imperfect.

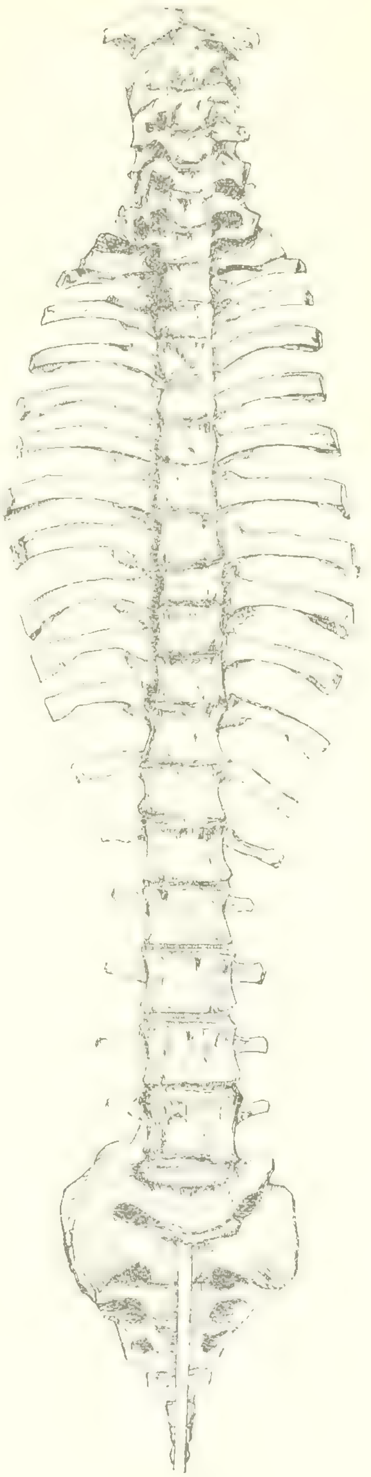
In some respects like the last, but an unsatisfactory specimen. There is nothing noteworthy in the neck or back. What is left of the 12th ribs, which have been cut, is perhaps rather unusually large, and placed a little high on the vertebra. The transverse processes of the 20th vertebra are very rudimentary and suggest that a small costal element has been lost. The change in the articular processes is below the 19th vertebra, and the spine of the 20th is exceptionally like a lumbar one. The spread of the lumbar transverse processes is greatest at the 22d and 23d. The 25th vertebra is sacralized on both sides, most so on the left, but apparently forms at most but a very little of the auricular surface, and on the right none at all. On both sides the lateral masses join those of the sacrum. On the right the line of junction is very plain; on the left the fusion is nearly complete. The promontory is very well defined below the 25th. From the front the sacrum appears normal, except that the *conjugata vera* is in the 4th piece; but from behind the 5th piece looks very much like a fused 1st coccygeal. There is but one detached coccygeal vertebra, the rest being lost. This one is nearly as large as it should be, but does not show the characteristic shape of a 1st one.

There is a general irregularity in this spine below the 19th vertebra. The condition might be well explained by Rosenberg's theory.

X. Cat. 9379–13.

Male, white. C. 7, T. 13, L. 5, S. 4, C. 4.

The spine is a very long one. It is remarkable for the asymmetry shown in various parts, which almost calls for a different notation for the two sides. The 13th pair of ribs is rudimentary. The right one measures 2.3 cm. and the left one 4. cm. The heads of both are almost wanting and rest on the pedicles rather than on the bodies. The left one has more the appearance of a rib; but they both are in a line with the ribs and rest on transverse processes. The 20th vertebra, to which they belong, has characters of both regions. The spinous process is distinctly lumbar, and the change of the articular surfaces occurs above it, though in a rather transitional manner. The spread of the lumbar transverse processes is greatest at the 3d lumbar (23d). The left transverse process of the 24th is that of a penultimate, but the right one is not. The 25th vertebra, sacralized on the right, is more asymmetrical than in any other spine of this class. Its body is separated from the sacrum by an uncommonly small disc, and there is a suggestion of a double promontory. On the left it presents a thicker transverse process than usual, but does not touch the sacrum. On the right the sacralization is complete. It seems at first as if on this side it were really the *fulcralis*, but closer observation shows it is not. Still it forms a considerable part of the auricular surface, which is completed by the two following vertebrae. This surface is shorter on the left, being borne wholly on the 1st and 2d sacral vertebrae. There are but four sacral vertebrae, though what is evidently a 1st coccygeal is fused with them. The lateral process of this latter is much more developed on the left, so as almost to form a fourth sacral foramen. The change of direction (*conjugata vera*) is on the 4th sacral. The three following coccygeal vertebrae were probably all distinct in the fresh state. Two of them are still movable. The greater development of the 13th rib, and of the lateral process of the 1st coccygeal, on the left, is noteworthy, as it shows an effort to preserve a normal lumbar and sacral region. On the right, where the sacrum rises higher, the 13th rib is smaller, and there are four distinct sacral foramina. The interpretation would at first seem to be: on the right 12 thoracic vertebrae; 5 lum-



X.

bars, the first with a free costal element, and 5 sacral vertebrae, counting as such the asymmetrical 25th, while on the left it looks more like 13 thoracic, 5 lumbar and 4 sacral, with 4 coccygeals. The fact, however, that even on the right the 25th is not the *fulcralis*, shows that the notation of the left should be adopted for both sides.

G–22. Cat. 9379–12.

Female, black, age probably from 20 to 30. The figure was remarkably good. C. 7, T. 13, L. 5, S. 5, C. 4.

In this spine the 25th vertebra is nearly free; but on the left its lateral mass, which shows distinctly a costal and a transverse element, has the latter close to the ilium, to which it is bound by ligament, but taking no part in the formation of the auricular surface. The right transverse process is very nearly normal and is distinctly separated from the ilium. There are 13 pairs of ribs. The first are not typical first ones, but narrower and somewhat like second ribs, though showing the scalene tubercle. The 13th pair are typical last ribs. The length along the anterior curve is 8.3 cm. for the right, and 3 mm. less for the left. The costal elements of the atlas on both sides are either undeveloped or lost. The former is more likely, for there is a small point at its usual place of origin and another jutting inward from the transverse process, so that the foramen is indicated, though open in front. (According to Macalister ('**93**) this occurs on both sides in .2%, and one side in 1.6%). The costal element of the 7th cervical vertebra is wanting on the right. There is no sign of a facet. The change in the articular processes occurs below the 20th vertebra, but its superior left process is somewhat transitional. The spinous process of this vertebra is distinctly lumbar. The spread of the lumbar transverse processes increases to the 3d. The next (24th) is a penultimate. It is doubtful if the 3d sacral touches the ilium. It has the *conjugata vera*.

Probably the most significant feature of this spine is the presence of 13 pairs of ribs, of which the lowest are typical last ones and the first not typical first ones. This would seem to be the first step of a moving of the thorax downward. It is to be remembered, however, that the right costal element of the 7th vertebra is wanting. Were there any signs of its having had a head and tubercle, this spine might possibly be correctly described as an archaic one. In their absence it may be that the freedom of this costal element, like that of those of the atlas, is simply accidental. The fact that the 24th has the characters of a penultimate lumbar in this class, is worth noting. It shall be returned to.

A–175. Cat. 9379–20.

Male, white. C. 7, T. 12, L. 6, S. 5, (C. 4?).

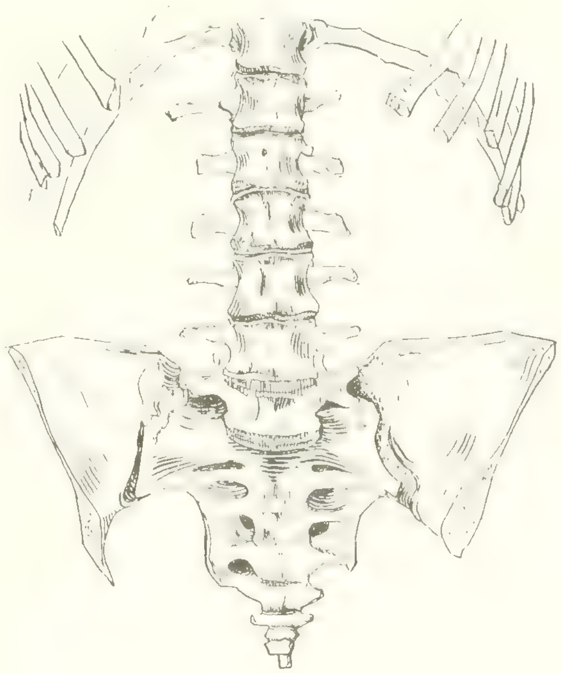
The extra vertebra is lumbar instead of thoracic as in the last. The 25th vertebra seems rather more free than in the preceding case. On the left the costal element touches both the sacrum and the ilium. It probably forms a small part of the auricular surface, but it seems lighter than in the other spine. The transverse process is nearly distinct from it. On the right the transverse process is separated from the ilium by a distinct space. The last ribs are long: the right, following the curve, 14.5 cm., and the left 13.2 cm. The change of articular processes is below the 19th, though the left lower joint is a little transitional. The spine of the 1st lumbar is rather thoracic. The spread of the lumbar transverse processes increases up to the 4th. The left costal element of the atlas is so rudimentary as to be almost imperfect. The 3d sacral does not touch the ilium. The *conjugata vera* is uncertain, but probably in the 2d. There are five pretty good sacrals, and three or four coccygeals, of which the 1st is hardly up to the standard.

2. Cat. 9379–41.

Female, C. 7, T. 12 (or 13), L. 6 (or 5), S. 5, C. 4.

This spine is very like the last two, but the nature of the 20th vertebra, which has free costal elements, is uncertain, and the 25th vertebra is almost free.

The 1st ribs are rather too slender to be typical. The 12th pair is long: the right one measuring along the front curve 14.2 cm., and the left 12.3 cm. The free costal elements of the 20th resemble transverse processes more than ribs, especially the left one. The right, which is curved, measures along the concavity 3 cm., and the left, which is straight, 2 cm. The change in the articular processes occurs below the 19th, but the lower processes are a little intermediate. The spine of the 20th is that of lumbar.



2.

The spread of the lumbar transverse processes, counting these as ribs, increases steadily to the 5th, but the difference between the lowest four is slight, and in the 24th they are delicate. The left costal element of the 25th vertebra projects downward from the transverse process to join the sacrum, but does not touch the ilium; neither does the transverse process. The latter is normal on the right. The five sacral vertebrae are probably normal, except that only two touch the ilium. The *conjugata vera* is at the 3d. There is a deficiency on the left of the 5th that is probably the result of an injury in preparation. The four pieces of the coccyx are small.

It seems that there is a pretty regular gain in the freedom of the 25th vertebra, shown in the spines of this class. In two the sacralization was about equal on both sides, in one it was entirely on the right, in three it was entirely, and in one chiefly, on the left. Were no other regions to be considered, the series of 25th vertebrae in this class might serve very well to illustrate Rosenberg's theory. In other respects, however, this series has many features that it is hard to group together. The 20th vertebra is by no means always alike, now more thoracic and now more lumbar. The 13th pair of ribs varies widely. In two cases (G–22 and 2) the 1st pair of ribs is under-developed. In the former there is a concomitantly strong development of the 13th pair which would imply a moving downward of the thorax; but in the latter there is only a slight development of the 13th pair. In one case the costal elements of the atlas are wanting on both sides, and in one rudimentary on one side. In the former of these (again G–22) the costal element of the 7th is wanting on one side. Spine X has an uncommon asymmetry of the two sides. Altogether this class is a very confusing one.

Class III.

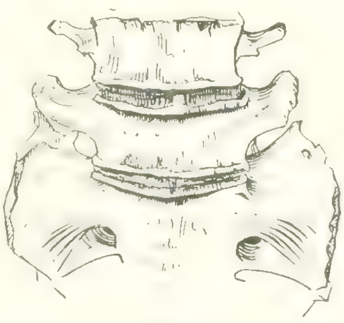
This class comprises the spines in which there are more than 24 perfect praesacral vertebrae. It is subdivided into three groups. In A the extra praesacral is thoracic; in B it is lumbar; in C the *fulcralis* is the 27th, so that there are two extra praesacrals. In the two cases of this anomaly one of the additional vertebrae is thoracic and the other lumbar. In both the last lumbar is sacralized on one side. The following spines are in Class III. Group A: 545, A–4, 764, 504, A–186, 578, 110. Group B: 493, Y, 381. Group C: 208, 297.

Group A.

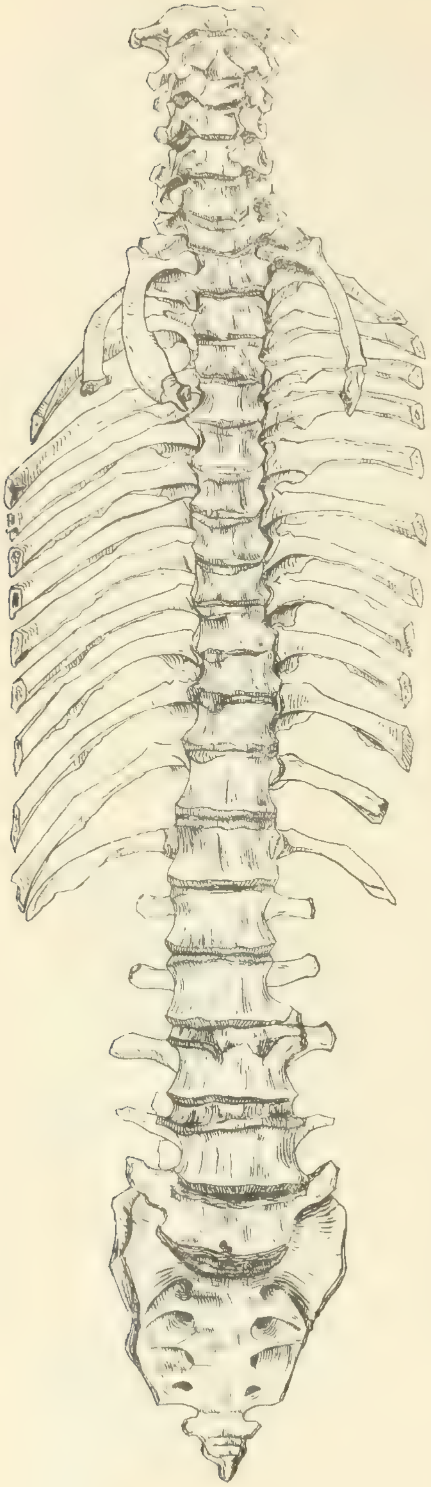
545. Cat. 9379–14.

Male, white, aet. 46. C. 7. T. 13. L. 5. S. 5. C. imperfect.

This spine is put first because both the transverse processes of the last lumbar vertebra approach so nearly, especially the right one, to the rising lateral masses of the sacrum that it almost belongs in the last class. On the right these parts are almost in contact, and closely connected by ligament, but there is no actual continuousness of bone. The costal elements of the 20th vertebra are very peculiar. The left one, about 3.3 cm. long, looks like a very thick transverse process the front of which rises from the side of the body of the vertebra. Looked at from the front, it seems very nearly in line with the ribs; from behind, in line with the transverse processes. In fact it represents both. The right one, some 3.8 cm. long, is more clearly a composite, for there is a hint of a head of a rib, and also of a separation between the two parts. Though these are absolutely one with the 20th vertebra, there is no doubt that the presence of a 13th pair of ribs is to be admitted. The change in the articular processes is below this vertebra. Its spine, moreover, is more thoracic than lumbar, in short very like that of a last thoracic. The lumbar region, except for the peculiarity of the last vertebra already mentioned, is very normal. The length of the transverse processes increases to the 3d, and the 4th (24th) is a penultimate. The 1st pair of ribs probably tends to encroach on the last cervical vertebra; but as they are detached, this is not absolutely beyond question. There is, however, no reason for doubting it, as this condition is shown in other spines of this class. The 6th and 7th cervical vertebrae present certain peculiarities. There are outgrowths of bone from the front of the bodies of both, but especially from the former, suggesting a lesion. Another from the root of the spine of the 7th extends upwards to the spine of the 6th. The transverse foramina of the 6th are double on both sides: a hole of the usual size having a small one behind it. The sacrum is of five pieces, but the first coccygeal and a part of the second are fused with it. The rest of the coccyx is wanting. The right auricular surface touches the 3d sacral, but the left stops just short of it. All in all we have a pretty normal spine with an extra thoracic vertebra. It was measured in the fresh condition, but the 20th vertebra, on account of the fusion of the costal elements.



545.



A 4

was at that time thought to be lumbar, and the measurements were made accordingly. The results compare as follows with the average of fifty male bodies.

	Length of 545.	Length, male average.	Proportions of 545.	Average proportions.
Neck	14.5 cm.	13.3 cm.	22.3%	21.5%
Back	28.3	28.7	43.5	46.3
Loins	22.2	19.9	34.1	32.2
Total	65.0	61.9	99.9	100.0

By transferring 3.5 cm., for a vertebra and disc, from the loins to the back we get the proportion of the back 48.9%, and of the loins 28.8%, which is about as much out the other way. It is worth noting that the proportion of the neck is nearly normal.

A–4. Cat. 9379–11.

Male, white. Evidently from an old person. There are exostoses on the spine and a slight twist. C. 7. T. 13. L. 5. S. 5. C. 3 or 4.

There are 13 pairs of ribs. The 1st left rib is rudimentary. The 13th are typical last ribs, which is uncommon. The 1st rib on the right is a tolerably normal one, but the left one is narrow, a little shorter than the other, and connected with its cartilage by ligament. The narrowest place, at the subclavian groove, is 8 mm. broad. At the end it is about 1 cm. The spine of the 6th cervical vertebra is bifid, which is rare among whites. The last rib of the right side is 8.5 cm. along the concavity, and that on the left 7.8 cm. The change of the articular processes from the thoracic to the lumbar type occurs below the 19th. The spine of the 20th is distinctly lumbar. On the other hand the spread of the lumbar transverse processes is greatest at the 3d (23d), and the next is a regular penultimate. The lateral masses of the sacrum extend upward towards the transverse processes of the last lumbar, so that this like the last represents a low degree of the freedom of the 25th vertebra. The sacrum and coccyx are all in one piece. Very little if any of the 3d sacral forms a part of the auricular surface. The change of direction of the surface occurs in the 3d.

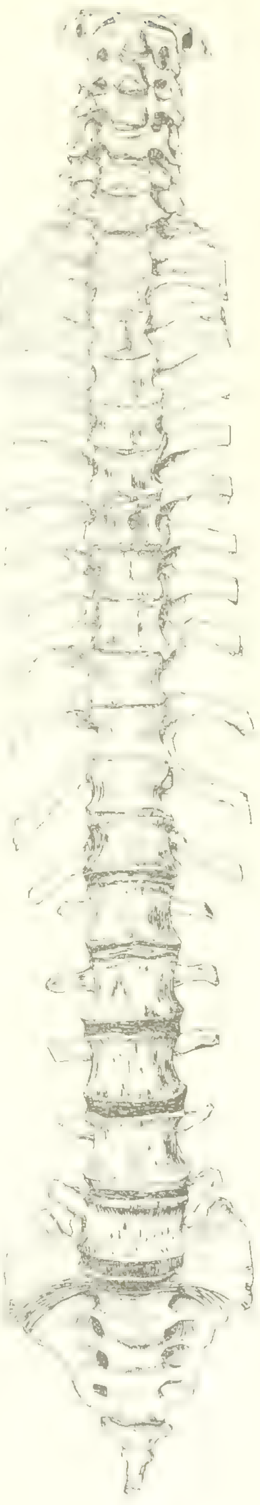
Here is an evident addition to the thorax with irregularities at both ends of that region. This can hardly be accounted for simply by the failure of the sacrum to advance. It is important to notice that instead of there being a concomitant enlargement of the left 13th rib with the undeveloped condition of the 1st left one, the former is smaller than its fellow.

764. Cat. 9379-8

Male, white, aet. 84. (The identity of this spine is not absolutely certain; that is to say it may not have belonged to a white man of 84, but it is a ligamentous preparation like the rest.) A part of the atlas has been cut away. C. 7, T. 13, L. 5, S. 5, (C. 5?).

The 13th ribs are each about 5 cm. long. The change in the articular processes is below the vertebra bearing them (20th), which has a spine approaching the lumbar type. The spread of the lumbar transverse processes increases to the 3d. The 24th and 25th are penultimate and ultimate lumbars. The five sacral vertebrae are very normal, except that the 1st has the lateral masses rising higher than usual. The change in the curve seems to occur in the 3d sacral. The auricular surface is on three vertebrae. The 1st piece of the coccyx is, perhaps, fused with the sacrum, but apparently this was a change due to old age. It is not fused with the others, which are united into one bone, probably consisting of four pieces; but this is not certain. The costal elements of the atlas are small, and on the left imperfect.

This spine is interesting as, while having essentially the same vertebral formula as the last, it is in many respects a more finished spine. In the last the sacrum tended to invade the loins, and both ends of the thorax were irregular. In this the sacrum, though tending to rise on the sides, does so much less, and the two ends



764

of the thorax are practically normal, as is also the lumbar region. It seems difficult under the circumstances to account for the extra vertebra otherwise than by an irregularity of segmentation in the thoracic region.

504. Cat. 9379–10.

Male, white, aet. 68. C. 7, T. 13, L. 5, (S. 6?), C. imperfect.

In many respects this spine is like the last. The 12th ribs, which have not been cut, are very long. The right one is 17.7 cm. following the curve, and the left 16.5 cm. The right 13th rib measures 3.5 cm., and the left 8.9. The latter is a perfect rib, but the right one is narrow and nearly straight. The articular processes change below the 19th vertebra. The spine of the 20th is lumbar. The spread of the transverse processes of the loins increases to the 3d on the left, though the difference is slight. On the right the 2d is rather more prominent than its neighbors. The lateral masses of the sacrum rise to near the transverse process of the 5th lumbar. The coccyx is imperfect. The sacrum on the left is clearly of six pieces, there being five foramina. On the right the fifth foramen is imperfect. The 3d sacral shows strikingly the change of direction. The coccyx is broken; what there is of it, one or two pieces, is fused with the sacrum. The spine is by no means so normal in its abnormality as the last. There are more transitional peculiarities at the junction of all the regions except the cervical.

A–186. Cat. 9379–46.

Male. C. 7, T. 13, L. 5, S. 5, C. (4 ?).

This is an old, distorted spine, with many exostoses on the front, connecting neighboring vertebrae. In most respects it is like the preceding ones, but a shabby specimen. The penultimate rib is long. The 13th ribs measure about 6 cm. and are certainly ribs. The change in the articular processes is below the 20th vertebra, the spine of which is lumbar. The 1st rib encroaches on the body of the last cervical. The bodies of the 2d and 3d thoracics are fused without exostoses, but it is probably pathological. The 3d lumbar has the greatest spread of the transverse processes, but those of the 4th lumbar are not typical. The lateral masses of the 1st sacral rise nearly to the transverse processes. The 3d sacral probably forms a minute part of the auricular surface. There is something of a transverse groove across its body. That of the 1st coccygeal is fused with the 5th sacral. The other coccygeal vertebrae are united, but their number is uncertain.

578. Cat. 9379–9.

Male, white, old. C. 7, T. 13, L. 5, S. 5, C. 4.

Like the last this is an old distorted spine with a twist and exostoses. The 1st ribs encroach on the 7th vertebra. The right 13th rib measures 6.6 cm. and the left 4.2 cm. Both the 12th ribs are long, but injured at the end. The change in the articular processes is below the 20th vertebra, the spinous process of which is thoracic rather than lumbar. The transverse processes of the loins increase to the 3d. The body of the 5th lumbar is co-ossified with the sacrum. This I consider a secondary pathological change; otherwise the spine would belong in the second class. On the whole the 5th and 4th lumbars are quite typical. The lateral masses of the sacrum rise considerably. The auricular surface is on three vertebrae. The front of the sacrum is remarkably flat. There is no change of direction at its 3d vertebra. The 1st coccygeal is fused with the sacrum. The remaining three are in one piece.

110. Cat. 9379–45.

Male, white, aet. 64. C. 7. T. 13. L. 5. S. 5. C. 4.

This spine may be very briefly described as not very different from others. The 12th pair of ribs (penultimate) is very long: measured along the concavity the right is 17.3 cm. and the left 17. cm. The costal elements of the 20th vertebra differ on the two sides. The right one is a diminutive rib, 3. cm. long. The left, also free, is straight, thicker, and more like a transverse process; it is about equally long. It does not reach to the body of the vertebra. The change in direction of the articular processes occurs below the 19th vertebra. The spinous process of the 20th is a typical lumbar one. The spread of the lumbar transverse processes is irregular, but the 24th and 25th are a pretty typical penultimate and ultimate. The sacrum and coccyx are normal. This again is a spine with an extra praesacral vertebra, with the 20th even more transitional than usual. Measurements were taken while the spine was still comparatively fresh, so that the discs had probably not lost any considerable part of their thickness. In the first column the 20th is counted among the thoracic, and in the second among the lumbar. The neck is somewhat too short in either case, as is to be expected with an extra praesacral. If the 20th be lumbar the proportionate length of that region is normal; but it is perhaps better to divide the error, as is the case if we consider it thoracic.

	Length of 110.		Length, male average.	Proportions of 110.		Average proportions.
Neck	12.7 cm.	12.7 cm.	13.3 cm.	19.5%	19.5%	21.5%
Back	31.7	28.6	28.7	48.8	44.0	46.3
Loins	20.6	23.7	19.9	31.7	36.5	32.2
	65.0	65.0	61.9	100.0	100.0	100.0

There is a general similarity in Group A. The most peculiar specimen is that of a rudimentary first rib. The boundaries of the thoracic region show a good deal of variation, sometimes being clear cut and at others transitional. Sometimes the 1st ribs encroach on the 7th vertebra. The lumbar region may, exceptionally, be practically typical.

Group B.

The spines in this group have the additional praesacral vertebra in the lumbar region.

493. Cat. 9379–18.

Male, white, aet. 37. C. 7, T. 12, L. 6, S. 5, (C. 4?).

The first ribs are large, as is also the 12th pair, which seems to occur in spines of this group as well as in those of the preceding. The right 12th measures along the curve 15. cm., and on the left 13.5 cm. The 20th vertebra has pretty nearly normal transverse processes. The change of the articular processes is, perhaps, a little transitional above the 19th, but typical below it. The spinous process of the 20th vertebra is thoracic rather than lumbar. The spread of the lumbar transverse processes increases to the 4th (23d), but they are all about equal. Those of the 24th and 25th are tolerably typical of the last two vertebrae. The sacrum is very normal except that the lateral masses rise, perhaps, a little too much. The auricular surfaces probably touch the 3d piece. There is no *conjugata vera.* The coccyx consists probably of four vertebrae, so fused together that the number is uncertain, but it can hardly be smaller.

Y. Cat. 9379–19.

Identity unknown. Male almost certainly. C. 7, T. 12, L. 6, S. 5, (C. 3 at least).

A very pretty spine. The 12th ribs are cut, but are probably longer than usual. The 20th vertebra has on the left a small transverse process, the nature of which is unquestionable. On the right a free process of about the same length (1.7 cm.), but broader, arises from a corresponding place at the junction of the pedicle and the lamina, clearly corresponding to the left one. The 20th, in the direction of the articular processes and in the shape of the spinous process, is a lumbar. The spread of the lumbar transverse processes increases to the 3d, below which it is pretty nearly the same. The 25th vertebra has the thick transverse processes of a last lumbar, and the 24th the puny ones of a penultimate, though they are not typical. The sacrum, except that the lateral masses extend very high, and that the canal is not closed in, is a normal one, with a well-marked promontory. The last lumbar faces more downward than is usual, but there is no false promontory. The 3d sacral presents a line across the middle of its anterior surface, marking a change of direction, and bears a part of the auricular surface on either side. There are certainly three coccygeals, possibly more. In the matter of proportions, judging from the dried spine in the want of fresh measurements, it is clear that the loins are too long. If the 20th vertebra were reckoned a thoracic, they would probably be too short.

There would seem to have been an error in segmentation by which there has been produced one lumbar vertebra more than usual. Except for one costal element being free, the 1st is tolerably normal, and so are the 24th and 25th, considered as a last two. With 6 vertebrae in the region in place of 5, it is impossible to reproduce the gradations of spread of the normal transverse processes. If this condition be due to the non-advance of the sacrum, how is it that the 24th has the features of a penultimate? That the 3d sacral vertebra is normal, is also noteworthy.

381. Cat. 9379 16.

Male, white. C. 7, T. 12, L. 6, S. 4, C. 5.

In many respects this is like the last, but the sacrum is less regular. The 20th vertebra is a normal lumbar vertebra in all respects, except that on the right there is a rudimentary costal element on the front of the transverse process, which is small and projecting beyond it. It probably was originally free. It does not reach the body of the vertebra. In its present condition, fused with the transverse process, the two do not equal the normal transverse process on the left. The spread of the lumbar transverse processes increases to the 3d. The 6th is a typical last vertebra, and the 5th a typical penultimate. The lateral masses of the sacrum rise so as nearly to touch the last lumbar transverse processes. Probably only two vertebrae form the auricular surface. The transverse line is in the 3d. The last coccygeal is fused with the sacrum, but probably this is a secondary change. There are only three pairs of sacral foramina. There are probably four other coccygeal elements, all fused together and now united with the 1st piece; but this union, like that of the 1st piece to the sacrum, is probably recent.

Group C.

This group contains two spines with two extra praesacral vertebrae, the 27th being the *fulcralis* and the 26th being sacralized on one side. The one first described is the only spine in this series which is not of my collecting. It was placed in the Museum by my grandfather, Professor John C. Warren, in 1847. It is very pathological. The second specimen was met with in the season of 1899–1900. It is also pathological, but much less so, and several of the changes, no doubt, occurred late in life; while in the former they are largely developmental.

208 (old catalogue number.). Cat. 9379–33.

Age unknown, but the spine is of a *man* who had reached, if not passed, middle life. The sex is determined by the pelvis.

C. 7, T. 13, L. 6, (S. 5 ?, imperfect).

Like all the others the specimen is ligamentous. The atlas is wanting, and the lower end of the sacrum is broken off. The right 12th rib is lost, but the cartilage-covered facet for the head is perfect. The sacralization of the 26th vertebra is on the right The spine presents a marked but not extreme spiral scholiosis, not easy to describe. It at first rises backwards and to the left, turning at the 2d lumbar to the right, and again to the left. The chief concavity is on the right of the lower part of the thoracic and the upper part of the lumbar regions. There is a much smaller compensatory curve to the left in the upper part of the back, and to the right in the neck. There are many compression changes of the vertebrae throughout the spine.

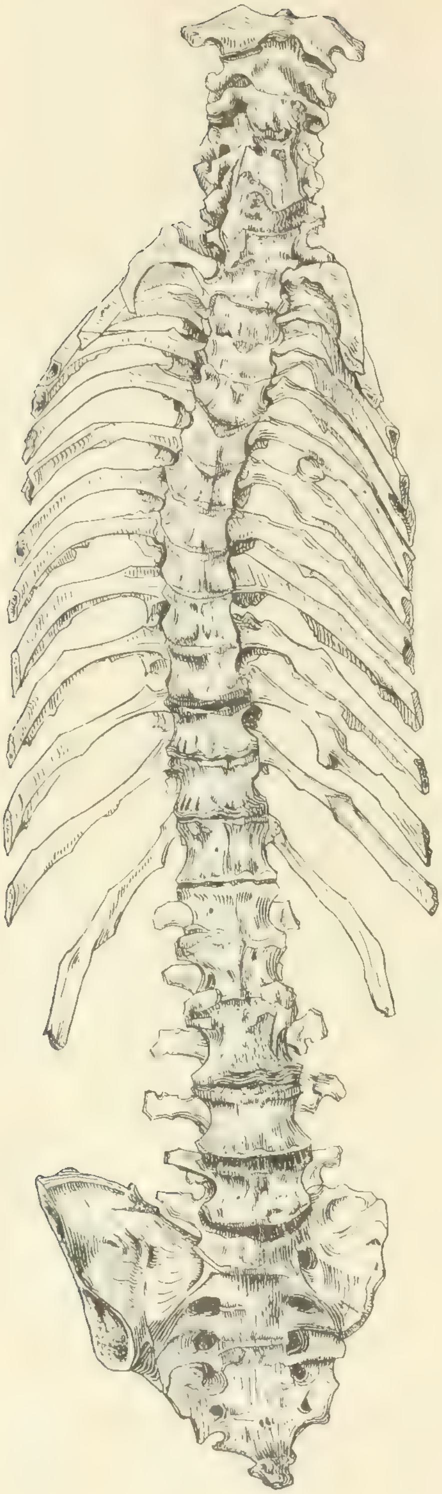
The spine is otherwise a pathological one, showing serious early derangement of the course of development. There is fusion of several vertebrae of the back and neck, and of the first three left thoracic ribs. An important feature is the great irregularity of the laminae of most of the cervical and of the upper thoracic vertebrae. The atlas is wanting, but there is nothing about the odontoid to suggest that it was peculiar. The laminae of the axis meet in the middle and are fused, as shall be described presently, with those of the following vertebrae, but below those fused with it there is want of union between the laminae of the two sides, as far as the upper part of the back.

The 2d, 3d and 4th vertebrae are fused at both the bodies and the arches. The left laminae are collected into one mass, the lower border of the 4th slanting strongly upward, while on the right, though fused, they are tolerably normal. The lower border of the 4th left lamina joins the upper part of the 3d right one. The lower part of the 3d and 4th right ones ends free at the median line. The bodies of the last three cervical and of the 1st thoracic are fused, but with their individuality preserved. The left lamina of the 5th is broadened and ends opposite to, but not touching, the fused right 5th and 6th laminae. On the right these are fused to the tip of the 7th spinous process. The left laminae of the 6th and 7th and of the 1st thoracic are fused, the last being slightly developed and not reaching the middle line. That of the 2d thoracic is very broad on the left and joins the right lamina of the 1st, making a spinous process projecting above that of the right 2d, which had no lamina meeting it on the left. Below this the arches are normal.

The bodies of the 3d and 4th thoracics are so completely fused, with but the slightest hint of a separation, that there can be little doubt of the condition having occurred at a very early period. There is, perhaps, some fusion between the bodies of the 4th and 5th and of the 5th and 6th, but in any case this is a pathological occurrence of late date.

There are 13 pairs of ribs. The first three left ones are fused into a single plate at, and beyond, the tubercles, which expands greatly at the distal end where it forks into two. The greatest breadth is 5.2 cm. As the sternum is wanting, the termination of the ribs is unknown. The 13th ribs are broken some 8 cm. from the heads. While their length cannot even be guessed, it may be said that they give the impression that they might have been several centimetres longer. What is certain is that they are not rudimentary structures. The change in the articular processes occurs between the thoracic and lumbar regions, i.e., below the 20th vertebra. The spine of the 1st lumbar is rather thoracic. The transverse processes of several of the lumbar vertebrae are injured so that the relative spread cannot be known. The left transverse process of the 5th (25th) is that of a penultimate, but the right one, though broken, is not. The 6th lumbar is sacralized on the left, touching the ilium. It forms, however, but a small part of the auricular surface. It shows signs of compression, and is not a normal nor a typical last lumbar. The next (27th) however, has the promontory above it and is evidently the 1st sacral or *fulcralis*. The sacrum is broken off obliquely through the 5th in such a way that almost all the ventral surface of that vertebra is lost. Its dorsal aspect is very like that of a fused 1st coccygeal. It is most probable from the appearance of the parts that the 4th sacral foramina were never completed below. The arch of the 1st sacral vertebra is incomplete on the left, but whether from want of development or from destruction by disease or violence, is hard to determine, though there are signs of injury. The auricular surfaces reach to the 3d sacral and perhaps extend slightly onto it.

While the spine is certainly very pathological, it is worth noting that the most serious disturbance of development is in the neck and upper part of the thoracic region; so that it is not clear how it should stand in any causal relation to the anomalous segmentation of the thorax and loins.



297.

297. Cat. 9379–52.

Male, white, aet. 85. C. 7, T. 13, L. 6, S. 5, C. 3.

This spine is an uncommonly large one, and shows signs of extreme old age. The bones are very friable, and in some cases have unfortunately suffered during preparation. There is a moderate twist in the back, but it perhaps is nothing more than a senile exaggeration of the curve in the cardiac region. Several of the ribs show united fractures; but it is safe to say that they did not occur in youth, and are too far from the column to be of interest in this connection. There is, besides the numerical variation, no marked disturbance in the ordinary process of development, except that the axis and the 3d vertebra are more or less fused. There is no disc between them; but it is impossible to say whether it may not have disappeared as several others have done; and the laminae are so intimately fused, especially on the right, as to point to a congenital union. The bodies of several others of the cervical vertebrae are connected by bony growths, while their arches are quite distinct. My colleague, Dr. Councilman, Professor of Pathology, agrees with me that the union of the bodies occurred late in life. That of the 2d and 3d, however, I regard as possibly congenital. It is known that these two vertebrae have a particular tendency to fuse. There are also several exostoses connecting bodies of vertebrae in the thoracic and lumbar regions. The last lumbar (26th) is sacralized on the left, and its articular surfaces fused with those below it. On the right the sacrum is fully co-ossified with the ilium.

In the neck the lowest four vertebrae are connected in front by outgrowths from the bodies, especially developed on the right, which have no morphological interest. The transverse and costal elements of the 7th are badly injured; so that it is not certain whether or not a free costal element existed on the left. Certainly, however, it was not a rib with even a minute head in a socket, but at most a continuation of the independence of a separate ossification. The appearance on the whole favors the theory of such a piece having been lost rather than broken off. The spinous process of the 6th vertebra is bifid. The body of the 7th seems larger than usual, but is, perhaps, not out of proportion to the large spine.

The thoracic vertebrae, 13 in number, are well formed in the upper part of the region, except for the senile exostoses which begin to appear at the borders of several of the vertebrae near the middle line. In the lower part these exostoses, though not individually large, are more numerous, causing a marked prominence at the edges of the bodies. There is also a suspicion of absorption of some of the bodies at the lower end. The 1st ribs are broken, but the head, neck, and tubercles on both sides are larger than usual, as, indeed, is the whole spine. The heads encroach on the body of the 7th vertebra. The last thoracic (20th) has a well-developed 13th pair of ribs. The left rib is about 12 cm. long, following the concavity. The right is longer, although broken at the end. The joint of the left one seems to have lost all motion, but there is no doubt that it once existed. That on the right retains its freedom. The head of the 10th rib rests against two vertebrae on each side. The same is true of the 11th on the left, but on the right the socket does not encroach on the 10th thoracic vertebra. The 12th rib is wholly on the same vertebra on the right, but on the left it certainly is against the disc above and perhaps touches the 11th vertebra. The 13th rib is certainly wholly on the same vertebra on the right, and probably on the left, but the head on both sides is much higher than is usual for that of the ultimate rib. The change in the articular processes occurs below the 19th vertebra on the left, but on the right the joint is rather transitional. The spinous process of the 20th is distinctly lumbar, but the transverse processes are those of a last thoracic.

The lumbar vertebrae are six in number, the last being sacralized on the left. Exostoses and moderate absorption of the bodies are most marked in the first two. The bodies of the 3d, 4th, and 5th, except for some exostoses at the top of the first, are very normal. The transverse processes are too much injured for accurate description; but it seems certain that those of the 3d and 4th are the longest, and that there is not the usual increase to the former and subsequent decrease. On the other hand the 5th has the small transverse processes of the penultimate. The 6th lumbar (the 26th vertebra) is certainly a praesacral. A very curious feature is that on the right the body of the 1st sacral vertebra rises nearly 1 cm. above the level of the lateral mass. The disc below the 6th lumbar is completely changed into bone, and from the size of the cicatrix can never have been of more than one third of the usual thickness. There is a double promontory above and below the 26th. The right transverse process is a typical one of a last lumbar. That on the left is very thoroughly sacralized, so that it is impossible to draw a line of separation through the lateral mass with absolute certainty. It seems, however, hardly possible by any *tour de force* to make the 26th the *fulcralis*; while the 27th may be made to include all, excepting perhaps a very small part of the whole of the upper region of the auricular surface, and in any case would seem to have the greatest share in supporting the ilium. The arch of the 26th vertebra is separated by a wide gap (1.5 cm.) from that of the 1st sacral, but in the middle the spinous process is continued down to unite with its tubercle. At the place of the articular processes the laminae are united so thoroughly that there is no sign of the joint. It can hardly be doubted that this union was congenital.

As for the sacrum, there is little else to say, except that the *conjugata vera* crosses the 3d vertebra, and the auricular surfaces end at about that level. The coccyx consists only of three pieces which are all fused together and also to the sacrum. The lowest piece is so large as to suggest that it is not the last, but there is no reason to believe that any were lost in preparation, especially as particular care was taken.

Here is a case of two extra praesacrals which is absolutely indisputable as far as the right side is concerned and, I think, beyond reasonable doubt on the left. Unlike the preceding case, there had been no great early disturbance of the course of development. I very deeply regret the uncertainty concerning the left costal element of the 7th vertebra, which is wanting, but which may have been injured. I myself believe it was lost. If it be so, this tallies with the somewhat higher position of the heads of the ribs on the left side of the vertebrae in the lower part of the thorax. There is an undoubted addition to the thorax, for the 1st lumbar is practically normal. Another remarkable fact is that, though the 26th is not a typical last lumbar, the 25th is practically a typical penultimate.

Cases of this kind are excessively rare. By far the best is the one which Zaaijer put at Rosenberg's service. There are 7 cervicals, the last bearing ribs, 14 thoracics, and 5 lumbars. While it is very much to be regretted that the preparation is not a ligamentous one, I, for my part, am strongly disposed to accept it. It is more nearly a normal spine, as regards pathological processes than any of the others. The next is my second case. My first one shows in the neck great disturbance of the early progress of the spine, and two of Varaglia's, in which there are several half vertebrae, a still greater. These, with the exception of some siren monsters are, I believe, all that have been described.

Class IV.

This class is composed of spines in which there is a tendency to the diminution of the number of praesacral vertebrae, which tendency, however, is not completely successful. In every case the 25th vertebra is the *fulcralis*. The spines of this class are divided into four groups.

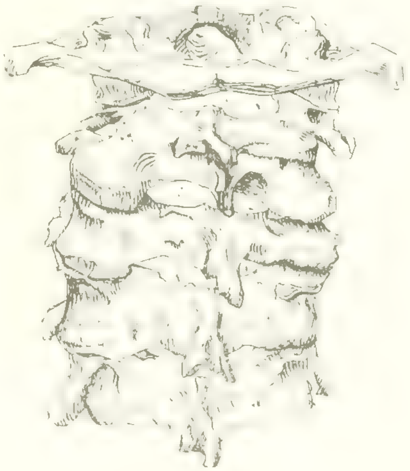
Group A consists of two spines in which there is more or less fusion of two or more vertebrae, which certainly occurred during the course of development. Group B consists of one spine in which the atlas is fused with the occiput. Group C also comprises but one spine, in which there is a diminution of the cervical vertebrae to six, which loss is partially compensated for by an additional lumbar sacralized on one side. In this latter respect the spine belongs in the next group, but it is put by itself on account of its great rarity. Group D consists of spines in which the last lumbar is more or less sacralized.

The spines in Class IV are the following. Group A: 264, Z; Group B: 24; Group C: H–3; Group D: 349, 492, 257, A–219, A–7, 141.

Group A.

Of the two spines in this class, the first evidently has great peculiarities dependent on a very early fusion of the elements of distinct vertebrae. In the second the process seems more distinctly pathological, and belonging to a later period.

264. Cat. 9379–51.



264

Male, white, aet. 88. C. 7, T. 12, L. 5, S. 5, C. 4.

This spine, besides some exostoses and fusions, probably due to advancing age, has one remarkable malformation in the cervical region. There is nothing worth noting below the neck, unless it be that the 1st coccygeal is fused with the sacrum and distinct from the other coccygeals. The fusion, on one side, of the lateral masses of the sacrum and the 1st coccygeal is complete.

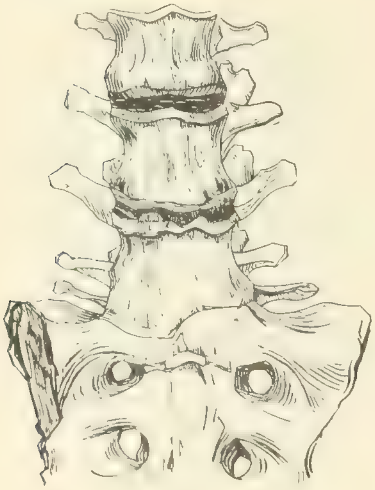
There are considerable irregularities of the nature of exostoses on the front of the bodies of the last two cervicals and of the 1st thoracic, with a diminution of the discs. (During preparation the cervical region became detached from the rest, but owing to these irregularities there is no possible suspicion of any error.)

The atlas is normal. The axis and the 3d vertebra have the bodies fused, that of the axis descending less deeply than usual. The total length of the axis is about 3.3 cm. The transverse processes of the 2d and 3d are, on the right, nearer together than usual, but with sufficient room between them for the passage of a good-sized nerve. On the left they are smaller and almost touching. The fusion of the laminae is complete; but while on the right there are evidently parts of two vertebrae, on the left they seem to be one, till close examination shows the duality. Two spinous processes are close together, of which the upper is bifid. In the region of the articular facets the depth of these fused vertebrae is decidedly greater on the right than on the left. The 4th vertebra is nearly normal on the front, but on the back the right lamina is reduced in size to make up for the greater size of the double one above it. The bodies of the 5th and 6th vertebrae are thoroughly fused, but their arches are distinct. How much of the fusion is a late pathological manifestation, I cannot say. Something in favor of this view is derived from a downward process, evidently of this nature, from the body of the 6th to the 7th.

It is very remarkable that there seems to be a particular tendency to fusion between the 2d and 3d vertebrae; and that there is a family likeness between the specimens.

Z. Cat. 9379–34.

Male, white, middle age. Nothing noteworthy was observed in the body before dissection. C. 7, T. 12, L. 5, S. 5, C. 3 or 4.



Z.

There is no reason to believe in any error of segmentation; but, probably during embryonic development, the last three lumbar and the 1st sacral vertebra were fused into one mass.

There is nothing to describe in the neck nor in the back, till we get to the 11th thoracic vertebra, the arch of which is ill formed, the laminae being narrow. Apparently there has been an inflammatory process in the joints of the left side, both here and in one or two vertebrae below. The change in direction of the articular processes is rather transitional, beginning above the 12th. The last ribs are short and narrow, especially the left one. The right is 5.3 cm. long and 1 cm. broad. The left is 4.2 cm. long and 7 mm.

broad. The bodies of the first two lumbars are normal, excepting that both are large and the 2d is particularly elongated. The spread of the transverse processes increases to the 3d. The body, arch, and transverse processes of the 3d lumbar at first appear perfectly normal, but the lower part of the vertebra is in front continued down, as a smooth mass of bone, to the sacrum, which it joins. From the back of the lower part of this mass are seen projecting on each side two rudimentary transverse processes. There is a roughness on the bone on the left, extending to the front from the origin of these two processes. On the right there is a smaller roughness, confined to the side opposite the 4th transverse process. There is but a vague hint of any interruption of the bone between the last lumbar and the sacrum, ever having existed. The arch and processes of the 3d lumbar are well developed, but it fuses below with the ill-developed parts of the 4th and 5th lumbars. The spine of the last is little larger than the tubercle which represents it on a normal 1st sacral vertebra. Indeed, it is only by some care that the arch of the last lumbar can be recognized, so completely is it fused with the sacrum. Of the latter there is little to say, except that the 1st coccygeal, distinct from the following ones, is fused with it.

Here, then, is a case of the want of development of the last two praesacrals, accompanied by their fusion with the adjacent elements above and below. What seems to me an effort, and a very successful effort, at compensation, is the fact that the change of the 12th thoracic to a lumbar vertebra for all practical purposes and the lengthening of the body of the 2d lumbar make a very respectable lumbar region, in spite of the rudimentary condition of two vertebrae, and of the loss of several discs.

Group B.

24. Cat. 9579 35.

Male, white. C. 7. T. 12. L. 5. S. 5. C. 4

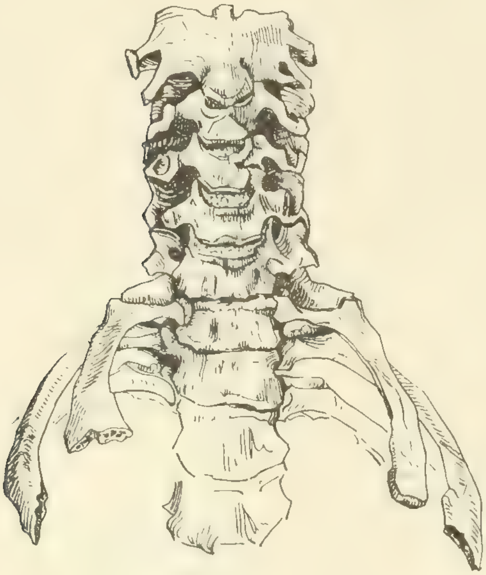
A remarkably normal spine, the only peculiarity of note being the tendency to diminution of praesacral vertebrae by the atlas being partially absorbed into the occiput. The bones are fused in front pretty symmetrically. The laminae forming the arch do not meet in the middle. The right one is free, and the left, which is less developed, is fused with the border of the foramen magnum. The 1st coccygeal is fused with the sacrum. The other coccygeals, at least three in number, are fused into one piece. There seems absolutely nothing else worth noting.

Group C.

H-3. Cat. 9379-40.

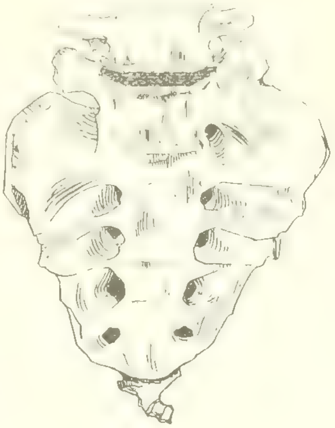
Female, probably old. (Insane.) C. 6, T. 12, L. 6, S. 6, C. 4.

This is a very remarkable, if not unique, case. There are only six cervical vertebrae, and of these the atlas and axis are fused. The fusion is so complete that the only points of separation are the intervertebral foramina. The odontoid, the anterior arch of the atlas, and its lateral masses are all indistinguishable. A projection 8 mm. long extends upward, above the rest, presumably from the odontoid. Its front surface is oblique, slanting upward and backward, and is smooth, as if having rested against some articular facet. The posterior arch of the atlas, however, is well developed and shows clearly the groove for the vertebral artery behind the articular facet. This facet is very far from normal. It is nearly plane, facing upwards, backwards and inwards. The right one, which is the higher and also the longer, is very slightly concave. It is unfortunate that we know nothing of the head. The 6th vertebra would pass as a very fair specimen of the 7th. It is not possible to speak of the 5th, for the tip of the spinous process is broken. The 7th vertebra is a 1st thoracic. The 1st pair of ribs, arising from it, is not perfect, but they seem undoubtedly to deserve the designation. The left one, with well-developed head, neck, and tubercle, measures 7 cm. in a straight line from the latter to the end of the shaft, which is rounded and free. By "rounded" is meant, not that it ends in a knob, but that the shaft retains its flatness, the outer and inner borders rounding off the angles as they turn to meet. The right 1st rib is cut, so that its termination is unknown, but there is no reason to doubt that it was a fairly typical 1st rib. The last ribs, the 12th pair, are decidedly long, considering the small size of this female thorax. The right measures 12. cm. and the left 11.5 cm. along the curve. There is a slight lateral twist in the upper part of the thorax, to the right. Several of the thoracic vertebrae have low bodies, as if compressed, and most of them are fused by a pathological process. There are several



H - 3.

exostoses in the places of the intervertebral discs. The change of the articular processes occurs below the last thoracic (18th) vertebra, the spine of which is decidedly lumbar. The 6th lumbar vertebra is clearly lumbar on the right, and very thoroughly sacralized on the left. There is a promontory both above and below the body, which is all but completely co-ossified with the sacral vertebra below it. The lateral mass on the left shows both a transverse and a costal element. The latter appears to form so large a part of the auricular surface that on the left this vertebra (the 24th) seems to be the *fulcralis*. The vertebra above it is on both sides very much like a last lumbar. The spread of the lumbar transverse process increases to the 3d, below which it is pretty nearly the same. The left transverse process of the 1st lumbar is smaller than the right. The 3d sacral vertebra shows the transverse depression across the body. It is doubtful if the auricular surface of either side touches this vertebra. The coccyx consists of four pieces. The 1st is well formed; the lower ones are confused and distorted to the left.



H 3.

In this spine we see that the thorax has moved upward and that the 6th vertebra is a typical last cervical. The 1st rib on the left is less like an ordinary cervical one than a rudimentary 1st thoracic. It resembles very closely the specimen of the latter in A–4 and in an imperfect specimen described later (9379–38).

It would seem, according to Rosenberg's views strictly interpreted, that while this spine is a primitive one in the neck, it is one of the future in the loins. He admits very frankly that the two processes working at the two ends of the spine do not by any means always hold the relation to each other that should be expected. Would it not be more plausible to say that the change at the two ends of the spine, instead of the discordant action of two tendencies, was the simple action of one,—in other words, that the last cervical vertebra becoming a thoracic, the last thoracic one becomes a lumbar, and the size of the thorax is retained?

Group D.

Six cases of partial sacralization of the 5th lumbar (24th). The spines differ among themselves in several details, as well as in the degree of sacralization; but they are arranged according to the latter, which is slight in the first and almost complete in the last.

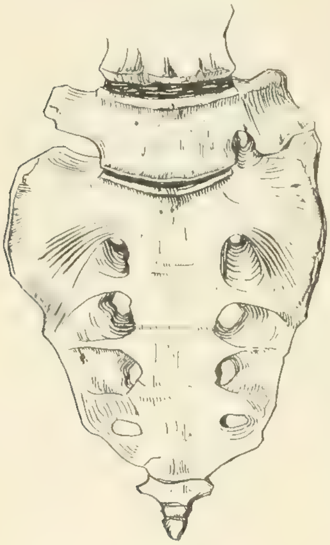
349. Cat. 9379–50.

White, female, middle-aged. C. 7, T. 12, L. 5, S. 5, C. 3.

There are irregularities at the junction of the back with the neck and the loins, and of the loins with the sacrum.

There is nothing remarkable in the neck except that there is a very minute *cervical rib* on the left. It is so thoroughly fused with the vertebra, and so small, that it is recognized with difficulty. It projects but slightly beyond the transverse process.

The 19th vertebra has the costal element free on the right, but without any distinct head, and looking more like a transverse process than a rib. The left one is fused. It is larger than on the right, and nearly like a normal transverse process. The right one measures 2.2 cm.; the left about 3.2 cm. Both of them are longer than the transverse processes of the following vertebra. The change in the articular processes takes place below the 19th. The heads of both the 10th and 11th ribs are higher than normal. The lumbar region, excepting the lowest vertebra, is very normal. Counting the 20th as the 1st lumbar, the transverse processes increase in their spread to the 3d. Those of the 4th are much smaller. In fact it is a typical penultimate. The 5th is normal on the right, but on the left it shows a low degree of sacralization. The outline of the transverse process is distinct above, but a downward projection of bone connects it with the top of the lateral mass of the sacrum, forming a large foramen. This vertebra forms no part of the auricular surface, which is entirely on the first two sacrals. The *conjugata vera* is on the 3d.



349.

The 19th vertebra is rather transitional, at least as far as its costal elements are concerned; but what is more remarkable is the tendency of each region to encroach on the one above it, on the left. Thus on the left the sacrum tends to join the last lumbar, the costal element of the last thoracic is fused, though larger than its fellow, and there is a small cervical rib. Thus there were probably once 12 free ribs on each side, but on the left the series begins and ends one step higher. The proportions require the 20th to be counted as a lumbar.

192. Cat. 9379 27.

Female, white. It was noted before dissection that the body was well formed and that the neck was long and thin. C. 7, T. 12, L. 5, S. 5, (C. lost).

There is a very small cervical rib on the left, with a minute head, neck and tubercle, and a small pointed projection in front of the latter. This rib is so closely connected by ligament that it is hard to make out that it is not fused with the vertebra. Even so, it doubtless was at one time distinct. There is a smaller and less characteristic costal element on the right, firmly fused. The heads of the thoracic ribs are placed high throughout: thus the 1st ones encroach somewhat on the body of the 7th vertebra, and the last ones are higher than usual. The articular processes change at the junction of the back and loins. The transverse processes of the loins are irregular, not following the usual plan; but some slight injuries make it impossible to measure them. The promontory is below the 5th lumbar. This vertebra is completely sacralized on the left, with, however, a distinct projection of the transverse process. On the right the transverse process rests upon the sacrum, but apparently without bony union. It does not reach to the region of the auricular surface. Seen from the front, it gives the impression that this vertebra must form a large part of the auricular surface, especially as a swelling at the base of the transverse process suggests that the boundary of the true pelvis begins upon it; but seen from the side, it is clear that it forms at most but an insignificant part of that surface, and that the vertebra below it (25th) is the *fulcralis* on both sides. The arch of the 24th is distinctly lumbar and not fused with the sacrum internally to the articular processes. The auricular surfaces on both sides just about reach the 3d sacral, which has the characteristic transverse groove. Below the last lumbar the sacrum is very normal.

It is to be noted that on the left, on which side the cervical rib is the larger, there is the greater tendency for the sacrum to rise, but the last thoracic rib is much smaller on the right. Thus this is an instance of the derangement of the concomitant variation often seen at the opposite ends of the thorax.

257. Cat. 9379–24. (Identity uncertain.)

Female, white. C. 7, T. 11, L. 6, S. and C. 8.

There is nothing remarkable in the neck and back, except that there are only eleven pairs of ribs. The last are cut so that their size cannot be known; but they are evidently very large for last ribs. The 19th vertebra is lumbar, the change in the articular processes occurring above it. The right transverse process is rudimentary, being a mere point. It is possible that a minute costal element was lost from that side. The 6th lumbar (24th) is strongly sacralized on the right, on which side it forms a large part of the auricular surface, but it probably is not the *fulcralis*. On the left it joins the sacrum, but does not articulate with the ilium. It forms with the 1st sacral a pair of foramina in the line of the anterior sacral ones. There is but the merest remnant of tissue between the body of the 24th and that of the 1st sacral, while the promontory seems to be above the former. There is an insignificant projection below it. There is probably some bony fusion of the arch of the 24th with that of the vertebra below, but the spine is distinct. After the 24th there are four sacral vertebrae, to which is fused the 1st coccygeal, forming a sacral foramen on the left but not on the right. Below this there are three coccygeal elements.

It is noteworthy that on the right, on which side the last lumbar seems all but sacral, the fifth following piece is less sacral than it is on the left.

This spine is one which has given me great trouble and furnishes a strong argument against the conception of a *vertebra fulcralis*. As has been shown, the 24th has nothing to do with the ilium on the left, and on the right *probably* does not form the largest part of the auricular surface, and therefore it is not the *fulcralis* according to the definition. Unfortunately this spine was not measured when fresh, but I have measured the front of the bodies of the vertebrae and compared them with the average of similar measurements on twenty spines. The table shows that without counting the 24th vertebra this spine is 1.7 cm. longer than the average, that the 11 thoracic vertebrae almost equal the usual 12, and that the lumbar region exceeds the normal one. Indeed the large size of these lumbars is very striking to the eye. Thus, although we must call the 25th the *fulcralis*, it is evident that, with the 24th in the sacrum, the spine has shaped itself after the fashion of a normal one, though with practically one praesacral too few.

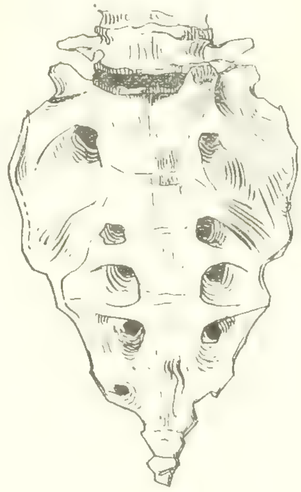
		Average height of bodies of 20 spines.		Height of bodies of No. 257.	
	3	1.2		1.2	
	4	1.2		1.2	
Cervical	5	1.2		1.1	
	6	1.1		1.3	
	7	1.3		1.5	
			6.0 cm.		6.3 cm.
	1	1.5		1.6	
	2	1.7		1.7	
	3	1.7		1.7	
	4	1.7		1.8	
Thoracic	5	1.7		1.9	
	6	1.8		1.9	
	7	1.8		1.9	
	8	1.8		2.0	

	9	1.9	1.9
Thoracic	10	2.1	2.2
	11	2.1	2.4
	12	2.3	
		22.1 cm.	21.0 cm.
	1	2.4	2.7
	2	2.5	2.9
Lumbar	3	2.5	3.0
	4	2.5	3.2
	5	2.6	3.2
		12.5 cm.	15.0 cm.
	Total	40.6 cm.	42.3 cm.

A-219. Cat. 9379-47.

Male, white. C. 7. T. 12 (11). L. 5 (6). S. and C. 8.

The only peculiarity in the neck is the excessive size of the body of the 6th vertebra, which is compensated by the smallness of the 7th, and that the spine of the 6th is forked. There are 11 pairs of ribs, the last being about 12 cm. long. The 19th vertebra is peculiar. The articular processes change below it. It has a normal transverse process on the left, but on the right this is more rib-like, being over 3 cm. long, and showing a tendency to bifurcate at its proximal end. There is no head, and it springs from the pedicle, but the bifurcation suggests a representation of a tubercle. The next four vertebrae are clearly lumbar; but the 24th is transitional, being sacralized on both sides. It, however, is to be counted as lumbar. The spread of the lumbar transverse processes, beginning with the 20th, is normal, and the 23d is a good penultimate. The sacralization of the 24th is further advanced on the left, where it forms a small part of the auricular surface. On the right it does not touch the ilium. There is a transverse element on each side, more isolated on the left than on the right. The body is completely co-ossified with the 1st sacral. There is a double promontory, of which the lower is the real one. The arch is quite distinct in the middle, with a well-developed spine. The 1st sacral (25th) is the *fulcralis*. There are eight pieces below the 24th vertebra, which seem to consist of 4 sacral and 4 coccygeal. There is a foramen between the sacrum and coccyx on the right, but on the left it is open. (An injury leaves the latter



A-219.

statement somewhat questionable, but it is made because certain appearances of the bone seem to justify it.) In this spine we have, as shown by the 19th, the 24th, and 29th vertebrae, a tendency for the sacrum and loins to move up higher on the left.

A–7. Cat. 9379–21.

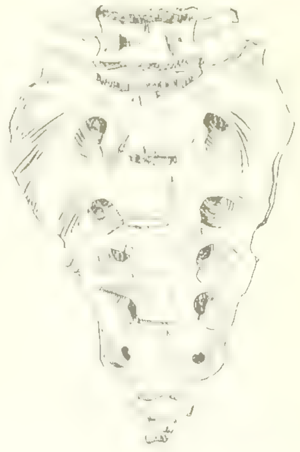
Male, white, aet. 64. C. 7, T. 11, L. 5, S. 5, (C. imperfect).

The cervical and thoracic regions present nothing noteworthy till we come to the 19th vertebra. This has on the right a transverse process of normal shape and origin, but unusually long and broad. The left one is of the usual proportions, but is free. The spinous process is distinctly lumbar. The change in the articular processes is above this vertebra, though rather transitional on the right. For these reasons I have decided to call the vertebra a lumbar, but with hesitation. The spread of the transverse processes in the loins is irregular; but owing to the twist of the spine and to some injuries of the processes the details cannot be given. The 23d is much like a last lumbar and there is no characteristic penultimate. There is a double promontory, above and below the 24th vertebra. It is hard to say which is the greater. The body of the 24th is partially co-ossified with the one below it, with some slight remnants of a disc persisting. The costal element, strongly developed on both sides, especially on the right, fuses with the sacrum. The arch is thoroughly absorbed into the sacrum, and the spinous process is replaced by a tubercle. These facts would induce one to call the vertebra sacral, were it not for its relations to the auricular surface. On the left it has nothing to do with it; on the right it forms a considerable part. Just how much is hard to determine; but I believe the 25th to be certainly the *fulcralis.* Below the 24th are five sacral vertebrae. The *conjugata vera* of v. Meyer is in the 3d. The extent of the auricular surfaces downward cannot be ascertained on account of injury. There is but one coccygeal vertebra, the rest having been lost. It seems to be partially fused with the sacrum, but this is probably a late-occurring change.

141. Cat. 9379–42.

Male, white, aet. 31. C. 7, T. 12, L. 5, S. 5, (C. 3 ?).

The neck and back show nothing particular. The change of the articular surfaces is between the 19th and 20th, except that the left superior joint of the last thoracic (19th) is somewhat transitional. The 20th vertebra is a typical 1st lumbar. The spread of the lumbar transverse processes increases up to the 3d. Those of the 4th are small, as is common in that vertebra. The 24th vertebra is the turning-point of the discussion, and is particularly interesting considered in connection with that of the preceding spine. It is very thoroughly sacralized. The promontory is above it. Below it is a faint secondary promontory with a very slight remnant of connective tissue in the middle. The lateral masses are well developed and nearly symmetrical. It is very hard to decide just how much of the auricular surfaces they form; but the left half of this vertebra forms so large a part of it as to make it very possibly the *fulcralis*, at least on that side. On the right it forms a smaller portion of the surface and is not the *fulcralis*. On the back there is a large interval between the arch and that of the next vertebra. Though there may be co-ossification at the articular processes, there seems no doubt that once there were true joints. Another reason for calling this vertebra lumbar is that in that case the *conjugata vera* passes through the 3d sacral. The coccyx itself is of an uncertain number of elements. The last sacral is rather transitional. It is curious that while with this spine there is more doubt which vertebra is the *fulcralis* than there was with the last, yet the arch of the doubtful vertebra in the preceding spine is much more incorporated with the sacrum than in this one.



141.

There are several spines in this Class in which one is much tempted to call the 24th vertebra the *fulcralis*, but I have adhered rigidly to the definition that the *fulcralis* is the one that forms the largest part of the auricular surface of the sacrum. In some of these this may be true of the 24th on one side. The greatest objection to the theory of the *fulcralis* is that (however this matter of the auricular surface may be) the 24th is practically a part of the sacrum, and that if the free portion of the spine is to be considered as an apparatus, the 24th must be left out of it, although it be not the *fulcralis*. It is also certain that in several of these spines there is a very transitional arrangement at the junction of the lumbar and sacral regions. The difficulty is a serious one; and should be frankly admitted. I was at one time disposed to reject the *fulcralis* on this account. The fact that instead of a certain vertebra we sometimes find one or more transitional ones, does not force us to deny the existence of that vertebra in a particular form in the immense majority of cases.

It must be admitted that the specimens in Group D of this Class tally very well with Rosenberg's view. The fact that the 23d so often has the features of a penultimate lumbar seems to me to speak for this interpretation, for I do not see how the assumption of sacral characters by the 24th, in the absence of a vital principle, can affect the details of the transverse processes of the 23d.

More difficult cases to account for in this way are found in the next class.

CLASS V.

This class comprises seven spines, in each of which there is a praesacral too few, the 24th vertebra being the *fulcralis*. In Group A, of three spines, a vertebra is wanting in the lumbar region. In B, of two spines, one is wanting in the back. In Group C, consisting of two very rare spines, there are 12 pairs of ribs, perfect at least on one side, and only six ribless vertebrae in the neck.

The spines are: Group A: D–7, 85, 377; Group B: 350, 478; Group C: 267, 202.

Group A.

D–7. Cat. 9379–26.

Male, white, very old. C. 7, T. 12, L. 4, S. and C. 9.

The spine is a very large one. The atlas is well shaped, but was evidently co-ossified with the occiput, though only a large fragment remains of bone partially filling the sockets and rising above the anterior arch. It is probable that this is a pathological change, occurring late in life. The 11th ribs are evidently very long, but having been cut, the length is unknown. The 12th pair are clearly ribs about 5 cm. long. The change of articular processes, however, occurs above the last thoracic (19th), which has a decidedly lumbar spinous process. The spread of the lumbar transverse processes is about the same after the 1st. The 24th or 1st sacral vertebra is thoroughly, and nearly symmetrically, sacralized. The promontory is above it, but there is a very slight false one below it. The arch is thoroughly incorporated with the next vertebra. Though the line of demarkation between this vertebra and the next below it in the auricular surfaces cannot be made out, I feel justified in calling this the *fulcralis*. The auricular surface rests on three vertebrae. The *conjugata vera* is probably in the 3d, though there is a hint of it in the 4th also. There are six pieces in the sacrum, but the last is probably the 1st coccygeal. Below this there are three pieces of the coccyx, of which the upper is free and the two lower fused.

From the 19th, inclusive, downwards the spine is peculiar with a general blurring of characteristics, and an increase of the transitional features. It was too much affected by the changes of age to permit measurements.

The theory of an undue advance of the ilium, and consequent disturbance of the regular progress of development, would in this case offer a very plausible explanation.

85. Cat. 9379–43.

Female, white. C. 7, T. 12. L. 4, S. and C. 10.

A delicate spine. Nothing to note in neck nor in back till the 12th thoracic is reached. The 12th left rib, about 4.5 cm. long, is clearly a rib with a head and a subcostal groove. The right one is lost, but there is a facet for the head on the root of the pedicle in a corresponding place to that for the left one. The change of the articular surfaces occurs above this vertebra (19th), but is rather transitional on the right. The spinous process is thoracic rather than lumbar. In the lumbar region the spread of the transverse processes is greatest at the 3d. The 4th has rather the appearance of the penultimate. The 24th vertebra is the 1st sacral. The promontory is above it, and there is the merest hint of a false one below it. On the right the transverse process is more outlined than on the left. On the left this vertebra is the *fulcralis* beyond any possibility of doubt; on the right it is less certain. The arch is fused with the rest of the sacrum. There is a faint line of change of direction across the body of the 3d sacral, at about the level of the lower borders of the auricular surfaces. The sacrum is of six pieces, but the last beyond question is the 1st coccygeal. It is thoroughly fused so as to inclose a fifth sacral foramen. There are four coccygeals below this, but the highest of them is too small to pass for a normal 1st one.

The following measurements were made on the fresh spine.

	Length of 85.	Average length, female.	Proportions of 85.	Average proportions.
Neck	11.8 cm.	12.1 cm.	22.5 %	21.2 %
Back	25.4	26.5	48.5	46.1
Loins	15.2	18.7	29.0	32.7
Total	52.4	57.3	100.0	100.0

Two things are apparent: first that the spine is a short one, second that another vertebra in the loins would go far to re-establish the proportions. Hence it is evident that the compensation in this case is slight.

377. Cat. 9379–25.

Female, white. C. 7, T. 12, L. 4, S. 5, C. 4.

A praesacral vertebra is wanting; but there is some doubt whether it is lost from the thorax or loins. There are 11 pairs of ribs, and the 19th vertebra has neither ribs nor transverse processes. The body has no certain facet for the head of a rib, but there is the suggestion of a small one on either side. It is probable that minute costal elements have been lost. The change of the articular processes is above the 19th, the spinous process of which is transitional. The transverse processes of the 20th vertebra are injured; but it seems that the spread in the lumbar regions is not normal. Those of the 4th lumbar (23d) are much like those of a last one; but there is no penultimate. The 24th is the 1st sacral and the *fulcralis*, with a distinct promontory above it, but its arch is more like a lumbar one than that of the 1st sacral should be. There is no secondary promontory. The auricular surfaces extend onto the 3d sacral. There is no *conjugata vera*. The sacrum has six vertebrae, but the last is evidently the 1st coccygeal. The 2d coccygeal is attached to the 1st, but the union is, probably, not bony. The 3d and 4th are fused together and separate from those above.

In the absence of measurements of the fresh spine the height of the bodies has been taken. It is clear that the proportions are rather more accurate if the 19th be counted as a thoracic and not as a lumbar. As far as its morphology goes, it could be put in either region.

		Average height of bodies of 20 spines.		Height of bodies of No. 377.	
	3	1.2		1.3	
	4	1.2		1.3	
Cervical	5	1.2		1.3	
	6	1.1		1.3	
	7	1.3		1.5	
			6.0		6.7
	1	1.5		1.8	
	2	1.7		1.8	
	3	1.7		1.8	
	4	1.7		1.8	
Thoracic	5	1.7		1.8	
	6	1.8		1.9	
	7	1.8		1.8	
	8	1.8		2.0	
	9	1.9		2.0	
	10	2.1		2.2	
	11	2.1		2.3	
	12	2.3		2.6	
			22.1		23.8
	1	2.4		2.8	
	2	2.5		2.9	
Lumbar	3	2.5		3.1	
	4	2.5		3.2	
	5	2.6			12.0
			12.5		
Total			40.6 cm.		42.5 cm.

This seems a very good instance of the suppression of a praesacral vertebra, the 24th being the *fulcralis*, though its arch is not typical.

(I feel called upon to mention that this spine fell into two pieces, parting below the 19th vertebra, which are now artificially joined. The accident happily did not occur in the original mounting, but subsequently, so that it is certain that no vertebra has been lost.)

Group B.

350. Cat. 9379–23.

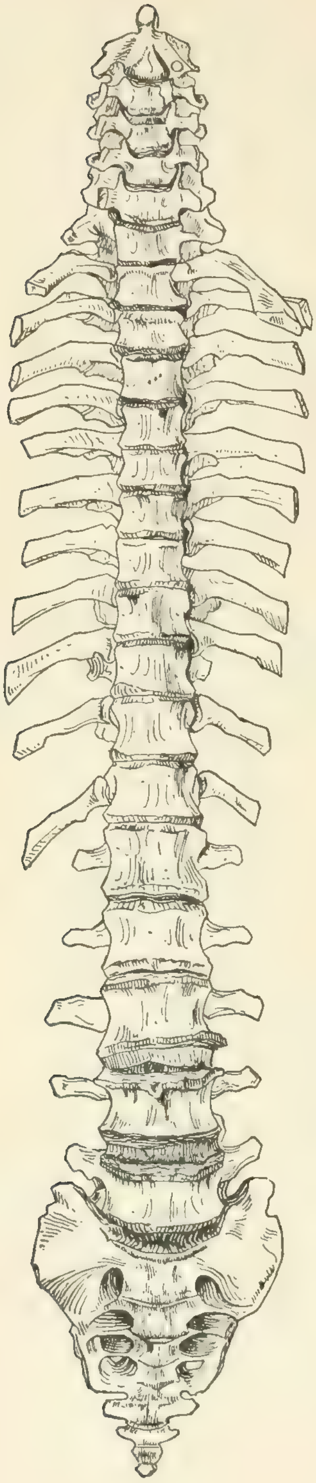
Female, white. C. 7, T. 11, L. 5, S. 5, C. 5.

There is nothing noteworthy in the neck. There are only 11 thoracic vertebrae. The ribs are cut, but the 11th pair is probably larger than the usual 12th one. The 18th is very nearly, if not quite, a typical last thoracic. The head of the rib is in about the normal place for that of the last one, and the head of the rib above it for that of the penultimate. The change of the articular processes is below the 18th. The spread of the lumbar transverse processes is irregular. The last lumbar (23d) has the appearance of the penultimate.

The 1st sacral is in some respects rather transitional. There is a distinct promontory above it, and a slight secondary one below it. The transverse processes are too clearly defined. While I believe it to be the *fulcralis*, I must admit that there is a want of absolute certainty. The arch is very thoroughly fused with the next vertebra on the right; less so on the left. The spinous process is too long. The articular processes descend onto the 3d sacral. The interpretation of the lower part of the sacrum is rather difficult. There are seven pieces; but the last two are to be considered as coccygeal. A lower detached portion of the coccyx probably consists of three pieces. The fusion of the first two pieces both with each other and with the sacrum, is very thorough. There are five pairs of sacral foramina.

Again in the absence of fresh measurements we have recourse to the height of the vertebral bodies. It will be seen that by transferring the 1st lumbar to the thorax, the proportions will become a little more normal; but in view of the reasons for considering the 19th a lumbar it does not seem advisable to make the change.

		Average height of bodies of 20 spines.		Height of bodies of No. 350.	
	3	1.2		1.2	
	4	1.2		1.1	
Cervical	5	1.2		1.3	
	6	1.1		1.2	
	7	1.3		1.5	
			6.0		6.3
	1	1.5		1.6	
	2	1.7		1.8	
	3	1.7		1.9	
	4	1.7		1.8	
Thoracic	5	1.7		1.8	
	6	1.8		1.8	
	7	1.8		1.8	
	8	1.8		1.9	
	9	1.9		2.0	
	10	2.1		2.1	
	11	2.1		2.3	
	12	2.3			
			22.1		20.8
	1	2.4		2.6	
	2	2.5		2.8	
Lumbar	3	2.5		2.9	
	4	2.5		2.8	
	5	2.6		2.9	
			12.5		14.0
Total			40.6 cm.		41.1 cm.



478.

478. Cat. 9379–22.

Male, black, aet. 41. Height 154.2 cm. Well shaped. C. 7, T. 11, L. 5, S. and C. 9.

Atlas lost, but axis quite normal. Nothing remarkable in neck, except that the right costal element of the 7th vertebra is imperfect. The ribs being cut, the size of the last is unknown, but they probably were large for last ones. The position of the heads of the 10th and 11th pairs of ribs were those of a normal 11th and 12th. The last two thoracic vertebrae are nearly typical. The change of articular processes below the 18th is rather transitional. Excepting this, the 10th and 11th thoracics are like the normal 11th and 12th. The head of the 9th rib is more symmetrically placed between two bodies than that of the antepenultimate should be. The spread of the transverse processes of the loins is normal, increasing up to the 3d. The 5th lumbar is much like a last one, but the 4th has not the characteristic transverse processes of a penultimate, though they are more slender than those above or below them. The sacrum consists of six vertebrae, of which the last is to be reckoned the 1st coccygeal. It is thoroughly fused, but does not complete a pair of sacral foramina. The 1st sacral (24th) is a typical *fulcralis*, with the promontory above it. It is quite sacral behind, and, indeed, would be perfect were it not that the transverse processes are a little too well defined. The auricular surfaces extend at least half way down the 3d sacral. The three lower pieces of the coccyx are fused into one.

From measurements made on the fresh spine we can compare both the actual and the relative length of the regions with the average. In so doing we ignore the fact that this spine came from a negro.

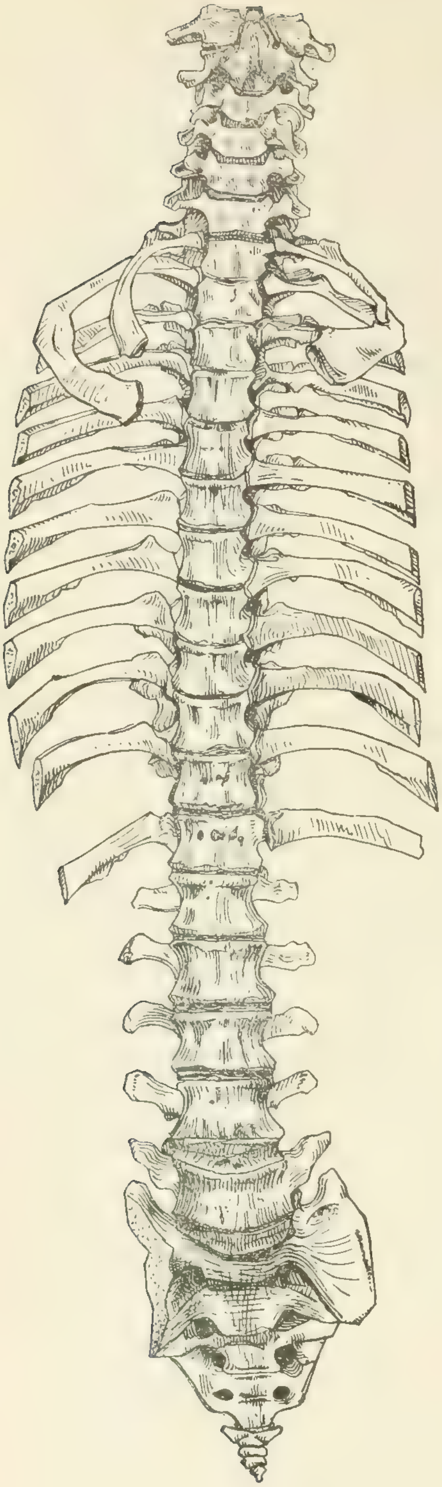
	Length of 478.	Average length, male.	Proportions of 478.	Average proportions.
Neck	12.6 cm.	13.3 cm.	22.0 %	21.5 %
Back	25.6	28.7	44.6	46.3
Loins	19.2	19.9	33.4	32.2
Total	57.4	61.9	100.0	100.0

It is clear that there has been but a slight effort to compensate for the want of a vertebra in the back by a greater height of the persisting ones.

This specimen is a very important one. Not only is the 24th evidently the *fulcralis*, but in spite of the absence of one thoracic vertebra, the lower end of the thorax is almost typical and the same may be said of the lumbar region. Should anyone doubt that the 24th may be a *fulcralis* I should refer him to this specimen with perfect confidence. The spines of Group B of the last class and of Groups A and B of this one are in a tolerably good series to show the progressive sacralization of the 24th. Holl in 1882, although not denying that the 24th might be a *fulcralis*, declared that he had never seen it. I was first inclined to put in Class V two spines that are now in Class IV. At first I thought the 24th the *fulcralis*, and later decided that it probably was not. In all the cases in this class I believe the 24th is the *fulcralis*, but I feel that in one or two instances it might be difficult to prove it to any one who refused to accept it.

Group C.

The next two spines are both very remarkable. On one side each has a perfect rib from the 7th vertebra to the sternum, and the second specimen has the next rib on that side passing to the junction of the manubrium and body of the sternum. One would be almost inclined, especially in the latter case, to classify them as wanting a cervical vertebra, but the cervical rib in both cases is imperfect on the other side. It is held therefore that a thoracic vertebra is wanting.



267.

267. Cat. 9379–30.[1]

Male, white, aet. 20. Height 170.5 cm. C. 7, T. 11, L. 5, S. 5, C. 4.

This spine has an absolutely unique malformation of the atlas that shall be described after the other peculiarities.

The 6th cervical vertebra has a long spinous process like that of the normal 7th. The anterior transverse tubercle is large on the left (on which side the cervical rib is less developed), and small on the right. The body of the 7th cervical is deeper vertically than that of the average 1st thoracic. It has a facet for the head of each cervical rib near the top of the body, and a slight upward deflection of the lower border above the socket for the head of the 1st thoracic rib. The spinous process is a repetition of the preceding. Seen from behind, the transverse processes rise towards their ends like those of a 1st thoracic, which on the whole the vertebra resembles very closely.

The 8th vertebra has nearly a whole costal facet above, and a very small part of one below. The upper surface is plane, instead of being concave transversely, as a first thoracic should be. The spinous process also is more compressed towards the end than that of a 1st. The 16th (9th thoracic) is like a 10th in having no facet on its lower border. The 17th bears on the right the whole of the head of the 10th thoracic rib, but on the left the facet extends onto the disc above. The transverse processes have facets for the costal tubercles and resemble those of the 10th thoracic more than those of an 11th. The 18th (11th thoracic) is almost a typical last one. The change of the articular processes occurs below it. The spinous process is rather lumbar, but the facets for the heads of the ribs are a little too high. The lumbar vertebrae are, on the whole, very normal, but the transverse processes after the 1st have nearly the same spread. Those of the 4th lumbar (23d) are not those of a penultimate. The 5th is a good last lumbar. The sacrum, which is cut on the right, is very normal excepting, perhaps, for the too great rise of the transverse elements. The 1st sacral is evidently the *fulcralis*. The promontory is single and characteristic. The auricular surfaces just encroach on the 3d sacral. The change of direction of the surface of the sacrum occurs on this vertebra, but there is no distinct *conjugata vera*. The coccyx has four pieces and is quite normal, the 1st vertebra being typical.

---

[1] This spine was described (Dwight, '**87**) together with spine 306. By an unfortunate mistake, for which I am not responsible, the atlas of this spine was marked "case 1," the rest of this spine "case 2," and the other spine "case 3."

The 1st rib on the right, coming from the 7th cervical vertebra, is very like a normal 1st one placed a vertebra too high, except that beyond the tubercle it is rather small. A straight line from the back of the tubercle to the end measures 7.8 cm. The concave edge is 8 cm. long. The breadth a little behind the junction with the cartilage is 17 mm., a little less than usual. The costal cartilage when fresh was 5.5 cm. long. It joined that of the next rib, the two occupying all the lateral border of the manubrium and reaching that of the 2d thoracic rib. The 1st thoracic rib on the right is a good 2d rib, but uncommonly broad.

The first rib on the left is a cervical rib, with head, neck and tubercle nearly as large as those of its fellow, but with a small shaft which ends in a knob resting on the next rib at about its middle. It measures 6.5 cm. along the concave edge. A groove behind the terminal knob marks in all probability the course of the subclavian artery, and a very faint depression near the inner border of the next rib, that of the vein. This latter rib (i. e., that of the 8th vertebra) is very broad, measuring 2.2 cm. at the front, and even more further back where it presents a tubercle, apparently from a distinct ossific centre, presumably for the rhomboid ligament.

The left half of the sternum was lost. The right half shows an upward growth of the manubrium, on the side of which the head of the clavicle rests, above the level of the top of the 1st cartilage. The manubrium and the second piece are firmly grown together, but the others are all distinct. Seven ribs in all reached the sternum, and the next approached it very closely.

The lumbar region presents certain curious separate ossifications below the inferior articular processes, which they prolong downward. They are largest below the 2d lumbar, where the right one is 8 mm. long and 7 across. The left one is a little longer and narrower. A smaller one is found on the right below the 3d lumbar, and a still smaller one is found on the same side below the 4th. They suggest epiphyses, but are where there are normally none.[1]

The peculiarity which makes the atlas unique is the total absence of the anterior arch. There are cases in which it is represented by ligament or cartilage; but here it is simply absent, and the front of the odontoid occupies its place. A strong band, which might be called *odonto-atloid ligament*, extends from each side of the odontoid outward to each lateral mass of the atlas. The right posterior arch of the atlas is represented by a distinct piece attached at each end by ligament to the rest of the bone. Thus each half of the atlas can move independently of the other. The odontoid projects above the neighboring parts of the atlas and bears a smooth facet on its top, slanting forwards, which rested against a fibrous or fibro-cartilaginous mass separating it from a tubercle on the front of the foramen magnum, a spurious third condyle. The superior articular facets of the atlas were but very slightly concave, and the occipital condyles correspondingly flat.

It is unfortunate that no measurements of the spine were made while it was fresh, but those made on the dry vertebrae are very interesting as showing how the thorax, in spite of the want of one vertebra, has even more than the usual length by the greater size of the bodies.

		Average height of bodies of 20 spines.		Height of bodies of No. 267.	
	3	1.2		1.3	
	4	1.2		1.3	
Cervical	5	1.2		1.3	
	6	1.1		1.3	
	7	1.3		1.6	
			6.0		6.8
	1	1.5		1.8	
	2	1.7		1.9	
	3	1.7		2.0	
	4	1.7		2.1	
	5	1.7		2.2	
	6	1.8		2.2	
Thoracic	7	1.8		2.3	
	8	1.8		2.2	
	9	1.9		2.5	
	10	2.1		2.5	
	11	2.1		2.5	
	12	2.3			24.2
			22.1		

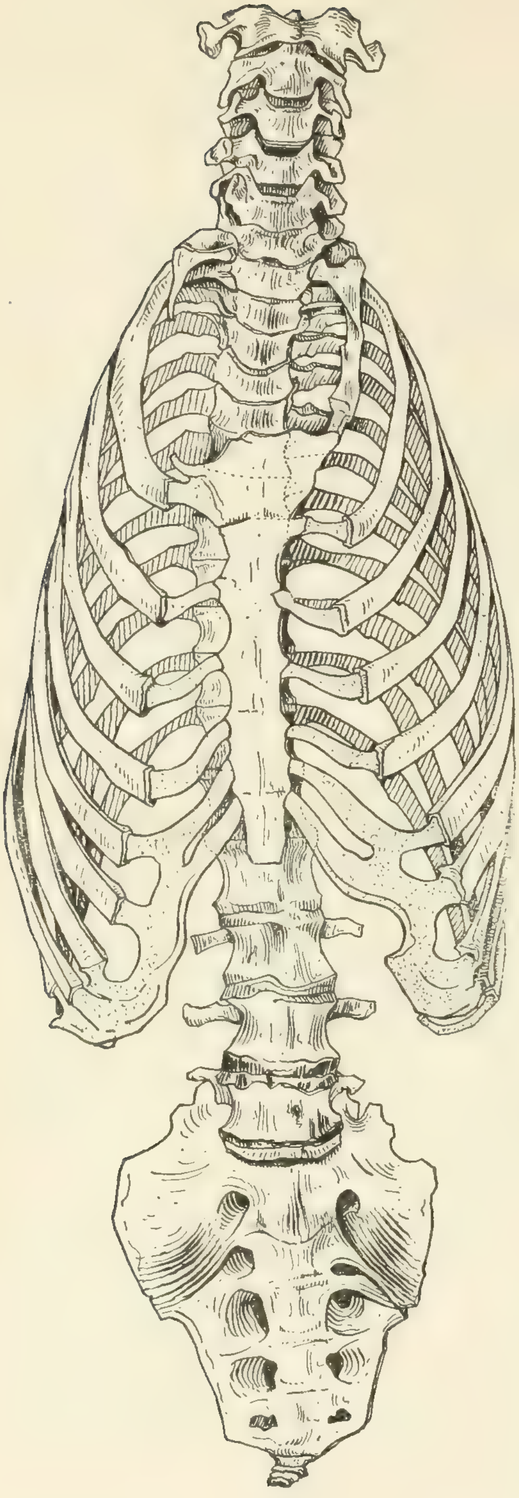
---

[1] These ossifications, as well as a part of the occiput, are figured in the Journal of Anatomy and Physiology (Dwight, '87).

	1	2.4		2.7	
	2	2.5		2.8	
Lumbar	3	2.5		2.6	
	4	2.5		2.4	
	5	2.6		2.7	
			12.5		13.2
Total			40.6 cm.		44.2 cm.

While the first pair of ribs is what are usually known as cervical, it might be permissible, in view of the fact that the subclavian artery on each side passed above them, and in view of the large size of the 7th vertebra and of its transverse process, to say that one cervical, rather than one thoracic vertebra, is wanting. This spine is remarkable as an instance of irregular segmentation, one vertebra being suppressed, while the lumbar, sacral and coccygeal regions are almost typically normal. Rosenberg has apparently overlooked my previous description of this case, for in his paper ('99) he alludes to a similar but less complete case of Gruber's; and does not seem quite convinced that the observation is exact. According to his scheme this case is to be described as one with a primitive condition of the lower part of the neck; while the lower part of the thorax and all below it have reached almost the maximum of transformation in the direction of the future. It may be questioned whether the almost typical condition of the lower half of the spine (apart from the numerical position of the vertebrae composing it) does not point to a condition that has suffered no change. Probably Rosenberg would reply that it is precisely this question of the numerical position of the vertebrae that is important. To express this differently: let us suppose that the spine had been divided in the middle of the thoracic region and the upper half lost. On examining the lower half all would agree that it is practically a normal spine, because no one would know that the last thoracic is the 18th vertebra, and the last lumbar the 23d. It would be taken for granted that they are the 19th and 24th. It does not seem to me plausible that an excessive progress of the ilium should have been accompanied by modifications that reproduce so nearly perfectly the normal conditions. There is an error of the original segmentation.

This spine furnishes two independent pieces of evidence in favor of vitalism. One is the increase in size of the thoracic vertebrae, by which eleven more than take the place of the normal twelve. The other is the development of the ligaments passing from the sides of the odontoid to the atlas, thus retaining it in position and allowing it some motion. At the same time mention should be made of the modification of the joints between the atlas and the occiput. What made all these concomitant modifications but an influence within the organism regulating the details of growth for the needs of the whole?



202.

202. Cat. 9379–53.

Female, white, aet. 75. C. 7 (6), T. 11 (12), L. 5, S. 6, C. imperfect. The sternum and costal cartilages are in place.

The interpretation of this spine is not easy, especially as the sides differ. There is some reason to hold that a cervical vertebra is wanting, as the arrangement of the ribs and the costal cartilages shows that the left rib from the 7th vertebra is a more perfect rib than any cervical rib yet described. The sacrum is less normal than that of the preceding specimen. The bones were extremely friable, which must excuse some injuries received in the preparation. There is a moderate scholiosis in the upper part of the back, the convexity being to the right. The left side of the chest is more prominent in front. The manubrium is very asymmetrical. The left half is about normal, except that the clavicular notch is more on the top than it should be, and reaches almost to the middle line. On the right the notch is very obliquely placed on the outer border of the bone; its lower border being more than half an inch below the level of the left one. The inferior border of the manubrium is a little lower on the same side.

The 6th cervical vertebra, seen from the front, is on the left like a last cervical in the small development of the anterior tubercle of the costal element (the anterior transverse tubercle). The parts were probably in the same condition on the right, but unfortunately are broken. The spinous process rather suggests that of a 7th, but not certainly. The 7th vertebra has on the left a rib which is continued by its cartilage to the normal place for the 1st rib, without any communication with the cartilage of the next. The course of the cartilage is peculiar inasmuch as it descends much more steeply than usual. The head, neck, and tubercle would do perfectly for a 1st rib, but the shaft is narrower, being at the end only 15 mm. It is placed very much on one side, so that the inner border is much more a superior one. The length from the tubercle to the outer border of the front end is 6.5 cm. in a straight line. There is a well-marked scalene tubercle with a very deep groove behind it. The groove for the vein is also deeper than usual. The 7th vertebra bears on the right a rudimentary cervical rib. The head, neck and tubercle are only about half as large as those of the left one. The shaft ends free in a sharp point, only 3.2 cm. from the tubercle. A curved, pointed projection, partly cartilage and partly bone, 18 mm. long, arises from the lower border of the right clavicular notch of the sternum and runs upward and outward as if to meet the rib. I am not aware whether there was any connecting ligament.

The ribs of the 8th vertebra are both peculiar. The left one, though ending by its cartilage at the junction of the manubrium and body of the sternum, is in shape like a 3d rib. The right one, though having a trace of a scalene tubercle and two faint grooves for the artery and vein, is a 2d rib in length, shape and direction, but rather broad at the end (2 cm.). It is inserted by its cartilage into the whole side of the manubrium from below the clavicular notch to the lower border. The body of the 8th vertebra is flat above like a 2d thoracic. The facet for the rib encroaches decidedly on the 7th vertebra on the right, and probably slightly on the left. The next ribs rest on two bodies, which condition continues to the top of the 18th vertebra. Seven ribs in all join the sternum on the left, and six on the right, besides the rudiment of the anterior end of the cervical one. The pair of ribs arising between the 8th and 9th vertebrae (the place of origin of the normal 2d thoracic) end symmetrically at the place of the normal 3d pair. Below this the arrangement of the cartilages is regular and symmetrical. The left rib on the 18th vertebra is about 15.4 cm. long, following the curve. The right one is broken, but also long. The heads are at the top of the body, encroaching on the disc above it. The 19th vertebra has a small transverse process on the left; but on the right there is the free head of a minute rib which is broken off about 1 cm. from its origin. It rests on the pedicle rather than on the body. The change of the articular processes occurs on the left below the 18th and on the right below the 19th, which is significant in connection with the condition of the first and last ribs. The 19th is the first to have a lumbar spinous process, though it is hardly a typical one. The lumbar transverse processes have the widest spread in the 22d. The 23d has rather small transverse processes and rather resembles a penultimate than a last lumbar. It is hardly possible to doubt that the 24th (the 1st sacral) is the *fulcralis*, but it is so thoroughly sacralized that the line of union of its lateral masses with those of the next below cannot well be made out. The real promontory is above it, but there is a slight secondary one below it. The arch is more free than that of a typical 1st sacral should be, and there is something of a spinous process. The *conjugata vera* is on the 3d sacral, but is not distinct. The auricular surfaces extend to the lower part of that vertebra. There are six sacral vertebrae, and the sacral canal is closed posteriorly till the last of them. There are five pairs of perfect sacral foramina. There seem to be at least three coccygeal vertebrae, but the end is broken. The 1st has a very slight development of the lateral parts.

It should be mentioned that the articular processes of the 22d, 23d and 24th, are more or less co-ossified on the right. The change is pathological.

The spine is very remarkable in many ways. In the first place the scholiosis would seem to be the result of the asymmetrical arrangement of the clavicles and ribs at the sternum.

The cervical rib of the left is the only instance in literature, of a rib from the 7th vertebra going to the sternum without joining the cartilage of the 1st thoracic rib, and of the latter going to the junction of the manubrium and body like a 2d rib. The most highly developed cervical rib, according to Gruber, has its cartilage reach the sternum in connection with the one below it. So far as I know, it never before has been seen to go alone. Naturally one is much inclined to call this a 1st thoracic rib a place too high. Were it double, there would be no escape from this classification. The presence on the right of a little projection from the sternum, as if to meet the small cervical rib, would seem to imply that the 1st rib on this side also was too high, but rudimentary, as it may be in its normal place. This view is strengthened by the resemblance of the 1st thoracic rib on that side to a 2d, and further by the 2d pair of thoracic ribs becoming a 3d pair at the sternal end.

The only approach to this case, unless H–3 is to be interpreted in the same way, is Albrecht's ('**84**), whose paper I have not seen. Pilling ('**94**)[1] in his notice of it puts the case in Gruber's ('**69**) fourth class in which the cartilage of the cervical rib joins that of the 1st thoracic. He says that its cartilage ends on a piece of bone which articulates with the sternum by a facet between the clavicular notch and the cartilage of the 1st rib. He does not state where the 1st thoracic ends.[2]

---

[1] Pilling carries on the bibliography from the point at which Gruber left it.

[2] After this paper had been presented to the Society of Natural History a case was published by Bolk (**1900**) in which the 7th and 8th vertebrae have respectively on both sides practically normal 1st and 2d ribs. The arrangement of the costal cartilages is absolutely that of the first two pairs. "*Sic transit*". . . . That is the end of the uniqueness of my specimen. I entirely agree with Bolk that the spine, which is practically otherwise normal, should be said to have six cervical vertebrae. I cannot, however, accept his explanation. He rejects excalation, which he interprets apparently as the disappearance in ontogeny, or perhaps the failure to appear, of one particular segment. He dwells on the complications that must ensue on

It is clear, however, that the travelling of the thorax upward has not been symmetrical; and that on the right (the side where it is less perfect) there is a small rib on the 19th vertebra, which on the left is lumbar, and that moreover the change of the articular processes occurs a vertebra lower on the right than on the left. This is another instance of the tendency for each side to have twelve ribs somewhere. On the left, where there is a good one in the neck, there is none on the 19th vertebra; on the right where that of the 7th is rudimentary, so as practically not to be a rib at all, there is a small one on the 19th.

The arrangement of the lumbar, sacral and thoracic regions in this spine is far less regular than in the preceding. It also, as far as the lower half of the spine is concerned, is far more consistent with Rosenberg's theory. Not so the upper part. This on the left is in some respects suggestive rather of the transformation of the 7th vertebra into a thoracic than of a cervical rib. The arrangement of the cartilages of the 1st and 2d left ribs is unique. On the other hand the shape of the rib from the 7th vertebra is strikingly like that of a cervical rib described by Gruber.

INCOMPLETE SPECIMENS.

The following specimens are incomplete. All except 7737.3, 8590, 132, 4767, and 1392 are, I believe, my additions to the Museum. While some of them are of little value, others are rare, and some of them fit in very well to supplement the complete spines.

FUSION OF THE ATLAS AND OCCIPUT.

Five specimens, of which the last is probably pathological.

7737.3.— An occipital bone and an atlas, evidently congenitally fused. The posterior arch of the atlas is open behind. The left side of this arch is much less developed than the other, and completely fused with the occiput except just behind the lateral mass

---

the loss of a certain segment, say the 6th, not only in the skeleton, but in the muscular and nervous systems. This is very just; but why assume that a certain individual segment is wanting?" Why not assume that between the occiput and the segment whence comes the 1st thoracic vertebra there has from the very beginning been one segment less than usual, and that the course of development has been correspondingly modified? Bolk's explanation is that the 1st segment, whence comes the atlas, is by no means very stable, and that the division between the occiput and the cervical region has in this spine occurred one segment too low. I have practically expressed in this paper my belief in the want of stability of the 1st segment; but what has become of it in this case? We are not told that there are any traces of it in the occiput. Even if it were found more or less incorporated with the occiput, it seems to me that it is expecting rather too much of the adaptive powers of nature to have a *perfect* atlas, as in this case, come from the segment below the one normally producing it, after the occurrence of an error in development.

where a foramen is found. The front arch is more or less fused with the skull. The lateral masses at the places where the joints should be are completely fused.

9638.— An old Egyptian skull of the 12th dynasty, probably male, four thousand years old, given me by Dr. John Dane. On the right the posterior arch of the atlas hardly projects from the level of the foramen magnum. On the left the arch is free but imperfect, ending posteriorly in a projecting point.

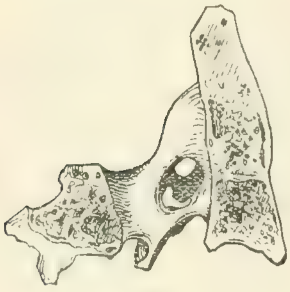
9639.— Base of a skull, probably male and white, from the dissecting-room a few years ago. It is almost the counterpart of the last, only the greater fusion of the atlas is on the left and the free point on the right.

8590 (Mason Warren Collection).— Probably white and female. Skull, with right half of atlas fused, left half wanting. The right half of the atlas is tolerably well developed. The front part is practically perfect, but ends sharply near the median line with a surface that apparently had been covered with fibro-cartilage. The posterior half is less developed, and ends before reaching the median line as a thickening of the border of the foramen magnum without any projecting point. The left half of the atlas evidently had been distinct, and was lost. The occipital bone on that side is practically normal with a rather low condyle.

132.— Skull, with atlas fused at the places of the joints. In other parts the atlas is well and symmetrically developed, and quite distinct. There is a hint of an old joint on the left. Probably the fusion is a pathological occurrence during life.

Fusion of Axis and the Third Vertebra.

4767.— The two vertebrae sawn through near the median line. The place of union of the bodies is very obscure on the front, but clear on section. The axis seems decidedly less long (vertically) than usual. The front view is nearly symmetrical, except that the transverse processes and the costal elements are nearer together on the left than on the right. The intervertebral foramina, seen from within, are about equal. While the laminae are quite fused, their duplicity is evident; and there are four tubercles at the end of the double spinous process. The length of the axis from the top of the odontoid is 3.5 cm., the total length of the two vertebrae 5.3 cm. A very curious feature, in view of an observation by Leboucq, which is considered later, is a linear fissure on the front of the right half of the specimen, which at first sight suggests a repetition of the joint between the atlas and axis. It appears,


4767.

however, that it is not between the axis and the fused vertebra, but in the former, and that, though in general transverse, it does not correspond to the line of the joint.

1392.—The two vertebrae uncut. On the front the place of union of the bodies is marked by what seems to have once been a disc, now thoroughly co-ossified with the bodies. That of the axis is very notably short, 3.5 cm. The total length is 5. cm. The left costal elements and transverse processes are very much nearer together than on the right, so as to make it highly probable that a nerve in passing out would be compressed, although, as in the preceding case, the foramina are about equal at the canal. The transverse foramen on the right is open laterally. Though there is a suggestion of injury, it is probable that the costal[1] element was never perfectly developed. The whole left side of the specimen is smaller than the right. The fusion of the laminae is there more complete. The spinous process of the axis is bifid. The right half of the spinous process of the 3d vertebra is present, the left one is wanting.

Probable Extra Half Sacral Vertebra.

9395-3.—The specimen is the left half of a sacrum and last lumbar, probably from a young person. The line of union of the lateral mass of the 1st sacral with that of the 2d, suggests that not impossibly it is a sacralized 24th. The lamina and spinous process of the 1st sacral are widely separated from those above, and though in apposition with those of the next below are not fused with them. Immediately below the tip of the spine of this 1st sacral is another, smaller tip, coming from the right, which evidently can by no possibility have belonged to a lower vertebra. It is quite distinct from the 1st sacral of the left, but fused with the 2d of that side. It can hardly be doubted that there was reduplication of half an arch.

Cervical Ribs.

725.2.—Obtained by me at Bowdoin, in 1873. A 7th cervical vertebra with a small rib on the left about 3.8 cm. long, ending in a point. On the right the costal element is wanting.

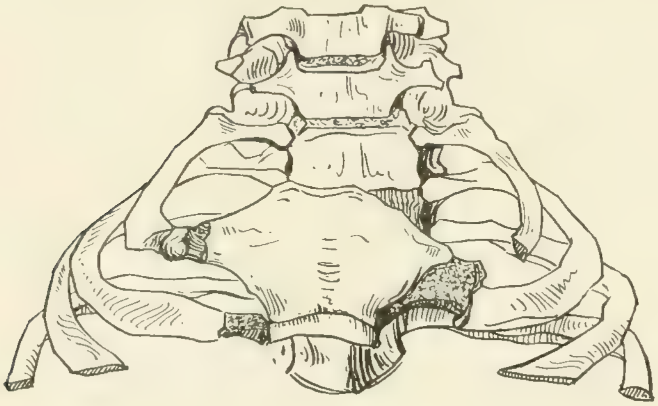
9379.37.—Male, white. A ligamentous preparation of the last three cervical and the first three thoracic vertebrae, with the proximal portions of the ribs. There is a pair of small cervical ribs, ending free. Measured in a straight line, the right one is 3.4 cm. long. The left one is probably about the same, but the end is broken. The small head of each rib rests on an outgrowth from the body some 4 mm. long. The spread of the transverse processes of the 7th vertebra is distinctly greater than that of the 1st thoracic. The slender neck of the 1st rib is uncommonly long; the transverse diameter of the costo-transverse foramen being about 17 mm. This specimen is a very striking demonstration of Lebouсq's view ('**96**–'**98**) that the cervical costal element is the piece of bone between the two tubercles. In the 7th vertebra the anterior tubercle is rudimentary, so that the costal element is relatively long and nearly transverse. In the 6th and those above it the costal element is short and directed more backwards, being the floor of the groove in which the nerve lies. The gradations are shown remarkably clearly. The 6th cervical is also remarkable. The foramen on the right is double. The anterior, which presumably is the costo-transverse, is not quite round. It measures transversely a little over 6 mm., and a little less antero-posteriorly. The transverse foramen, almost directly behind it, measures nearly 4 mm. On the left the foramen is large, measuring nearly 1 cm. in diameter. There is some indication of a notch at the posterior outer aspect, as if another were partly cut off from it. The foramen on the right of the 5th vertebra shows at the back a distinct attempt at a subdivision.

---

[1] This term is applied to the piece of bone forming the floor of the gutter for the nerve

Rudimentary First Ribs.

140. Cat. 9379.38.— Male, white, aet. 38. A ligamentous preparation of the last two cervical and the first four thoracic vertebrae, with ribs and manubrium. The first rib on the right is smaller than usual, especially at the part beyond the tubercle. It reaches to about 2.5 cm. from the sternum and is then continued by cartilage which contains a large distinct calcified piece. The left corresponding rib is much smaller. It is strongly curved. The head, neck, and tubercle are not excessively small, though smaller than those parts of the right rib. The distance from the outer edge of the tubercle to the tip in a straight line is 5.6 cm. The breadth near the front is under 1 cm. It ends free more than 4 cm. from the manubrium. Whether, as is most probable, it was connected by ligament, I am unable to say. The next rib is very like a normal 2d one, excepting in its insertion. The cartilage extends all along the side of the manubrium, and from the upper part of this cartilage there is a short projection towards the rudimentary rib. The



140.

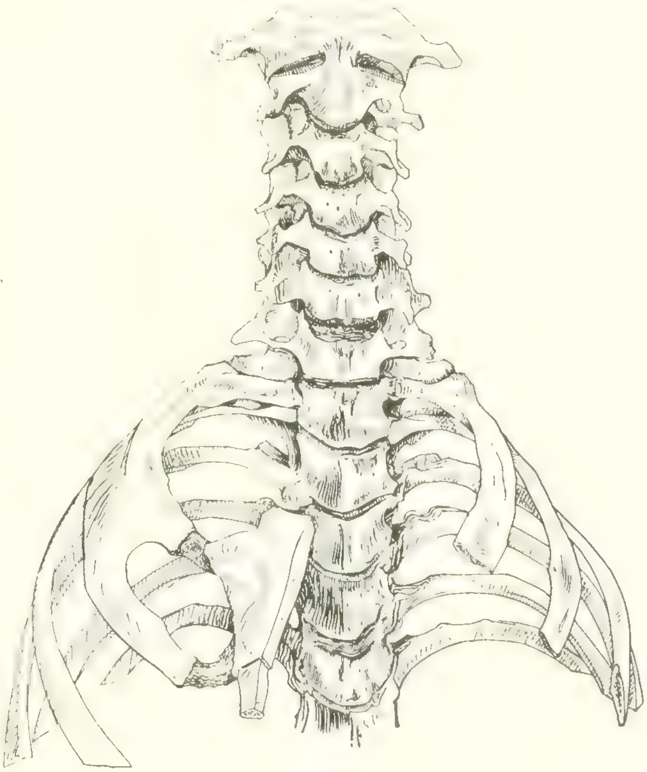
sterno-clavicular joint is lower and more oblique on the left. The subclavian artery evidently passed over the rudimentary 1st rib.

Except that the sides are reversed, this is exceedingly like the state of affairs in spine 202, only there we have a small pair of cervical ribs, and here a small pair of 1st thoracic ribs.

572.— Male, white, aet. 70. The specimen consists of the right half of the sternum, and of the right 1st rib, which is small and continued by ligament to a calcification of the cartilage near the manubrium. The distance from the end of the bone to the sternum is about 3 cm. There were six lumbar vertebrae.

FUSION OF FIRST AND SECOND THORACIC RIBS.

C–1. Cat. 9379–49. — This specimen consists of the cervical and upper part of the thoracic regions and of the right half of the upper part of the sternum. The spine was normal. The only peculiarity worth noting is presented by the first two ribs of the right side. The heads of both ribs rest entirely against the 1st thoracic vertebra, not encroaching on the disc either above or below it. The head of the 2d rib is much smaller than normal. There is but a slight interval between the two heads. The tubercle of the 2d rib also is very small and rests on a minute facet at the very upper corner of the end of the corresponding transverse process. At about 4 cm. from their origin the two ribs fuse into a broad plate, on which all marks of separation are gradually lost. A rudimentary scalene tubercle on its upper edge separates two slight grooves. The greatest breadth of the plate, 4.2 cm., is just before it divides into a short upper and a longer lower prolongation representing the terminations of the shafts of the ribs. Each is continued by a piece of cartilage to its normal termination.



C–1.

Of the deductions that may be made from these specimens, some are of merely morphological interest, while others are far-reaching. It is not possible to separate the two groups completely.

Terminal Vertebrae and Those at the Ends of the Different Regions of the Spine.— It seems beyond question that certain vertebrae are capable of having the characteristics of those above or below them in numerical order. The last coccygeal may be just the same to all appearance, though its number from the atlas may differ by several places. The last sacral and 1st coccygeal are absolutely uncertain. As the vagaries of the 24th, 25th, 26th, and even the 27th, any one of which may be the *fulcralis*, are at the basis of the classification adopted in this paper, they need not be discussed here, except in so far as the condition of a given vertebra affects that of others, as for instance the effect of a certain vertebra being the *fulcralis* on the two vertebrae above it and on the sacrum as a whole. It is rather surprising that no effort has ever been made to decide whether sacra could be distinguished one from another according to the particular vertebra that happens to be the *fulcralis*. From this series it would seem that there are certain peculiarities which in most cases would enable us at the very least to separate the sacra in which the 24th is the *fulcralis*, and those in which it is strongly sacralized, from those in which the 25th or the 26th is the *fulcralis*. On the other hand slight sacralization of the 24th and 25th may be very similar. While it is likely that a larger series would show more instances of difficult diagnosis, I think it would confirm the deductions from the present one, which are as follows:

Distinctions between Spines with Sacra of Different Numerical Composition.—

I. When the 26th is the *fulcralis* and the 25th more or less sacralized, the promontory is perfectly evidently above the former, and there is no secondary promontory. The 25th, apart from its sacralization, is a good last lumbar, the disc below it, though much diminished, is always present, and the 24th is always a penultimate. (The spine of a child of ten (spine 21) is the only exception to this rule. The promontory is not over-evident, nor is the possibility of a secondary one to be denied; but this, it is to be remembered, is a characteristic of the pelvis of early childhood. Spine X is very different on the two sides, and I hesitate to affirm that, if looked at from the right side only, there might not be doubt about the position of the promontory.)

II. When the 25th is quite free, the promontory is always unmistakably below it. The 25th and 24th are generally pretty typical ultimates and penultimates.

III. When the 24th is sacralized more or less, but is not the *fulcralis*, the position of the promontory is not clear, and sometimes very doubtful, being either above or below the 24th or being double. There is little or no remnant of a disc below the 24th. The free portion of the 24th is generally a part of a good ultimate, and the 23d generally a good penultimate.

IV. When the 24th is the *fulcralis*, certainly or probably, there is often a secondary promontory below it. The 23d may be a good ultimate or a penultimate, or it may present features of both. Thus the transverse processes may be thick and broad at the root, like those of a 5th lumbar, and toward the tips they may become light by the rising of the lower border, as in the 4th lumbar. The 22d is never a typical penultimate. That of spine 478 is the nearest approach I have seen. Perhaps the 1st coccygeal is more likely to be fused to the sacrum if the 24th be the *fulcralis* or be much sacralized, but I have great doubts whether its condition is of any value.

In brief it appears that the spine adapts itself much more easily to an additional praesacral vertebra than to the loss of one. In the former case, assuming that the addition is in the thorax, the 24th vertebra is or may be a very good penultimate lumbar, while in the opposite case it is not. Rosenberg alludes to a case of Tenchini, as possibly presenting this condition. I have not had access to it. In my series there is no perfect case. Both 478 and 267 approach the condition, and present lumbar regions which on the whole are not far from typical, but the more normal condition of spine 764, in which the 26th is the *fulcralis*, is evident.

The Variations of the 19th and 20th Vertebrae.—These are familiar to all who have studied this subject, but it may not be amiss to recapitulate some of them briefly.

In Class I, Group A, the 19th in G–19 is thoracic, with one costal element free but minute and the other fused like a transverse process; in 636 the 20th, as far as these features are concerned, is much like it; in 567 the 20th, though in most respects lumbar, bears ribs. In Group B, both in 729 and 306, the change of articular processes is above the 19th; the former seems to have transverse processes cut through at their bases, and the latter small ribs that have become fused so as closely to resemble transverse processes.

In Class II, in which the 25th vertebra is more or less sacralized, we find in 561 that the 20th is thoracic with lumbar-like transverse processes; that it is more lumbar in 361; that in X it is more transitional and hard to place, suggesting a different interpretation for the two sides; that in G–22, though rather transitional in some respects, the 13th ribs are typical last ones; and that in 2, though on the whole lumbar, it has free transverse elements.

In Class III, in which there are 25 free praesacrals, the 20th is held to be thoracic in Group A, and lumbar in Group B, but still in the development of the costal elements, the nature of the spinous process, and the place of change of the articular processes, there is absolutely no rule.

In CLASS IV, Group D, in which the 24th is more or less sacralized, the 19th is on the whole thoracic, but generally with lumbar or transitional features.

In CLASS V, in which the 24th is the *fulcralis*, we find in Group A that in D–7 the 19th has lumbar features and the change of the articular processes is above it, but that nevertheless it is reckoned thoracic. In Group B it is essentially lumbar in both spines. In Group C it is clearly lumbar in 267 and transitional in 202, differing on the two sides.

Apparently both these vertebrae are absolutely unstable. It is impossible to decide the number of an isolated one. A 19th may be a typical lumbar, and a 20th a typical thoracic.

I do not remember to have seen mentioned the fact that when the last ribs are very small or rudimentary, the pair above them is much longer than a penultimate usually is. This is true whether the last pair be on the 19th or the 20th vertebra.

Cervical, Rudimentary 1st Thoracic, Bicipital and Tricipital Ribs.— The anomalies of the region at the top of the thorax are both more interesting and more difficult than those at the bottom. There we have just seen that one vertebra may perfectly resemble another of a different numerical position; here it is more doubtful. From the study of these spines and the writings of others, it appears that there is at least one type of a rib which is seen only on the 7th vertebra, and that there is a peculiar form of bicipital rib which is seen only in the thorax. On the other hand, while several instances of defective 1st thoracic rib are very much alike, it is impossible to distinguish them with certainty from cervical ribs.

In this series there are ten spines and two incomplete specimens with ribs connected with the 7th cervical vertebra. This includes H–3 in which it is more probable that there is a suppression of a cervical vertebra, so that the 1st ribs, one of which is imperfect, should be considered thoracic. There is one case of bicipital rib (649). There are also the following cases of defective 1st thoracic rib: G–22, not rudimentary but small, A–4, H–3 (if it be not included among cervical ribs), and incomplete specimens 9379–38 and 572. Moreover there are the following cases of fused thoracic ribs: spine 208, tricipital; and incomplete specimen C–1, bicipital.

Among the cervical ribs (putting the doubtful H–3 aside for the present) there are two cases in which their cartilages reach the sternum (267 and 202). According to Gruber's classification the most perfect form of cervical ribs has the cartilage joining that of the 1st thoracic before reaching the sternum. There is, I believe, no single case on record of a cervical rib having its cartilage end at the place of the normal termination of the first rib, with the next rib ending at the junction of the manubrium and body of the sternum, and the cartilages being absolutely separate.[1] This is what occurs in 202, on one side. Moreover the rib in this case is peculiar, and remarkable in that it resembles closely one figured by Gruber. It is narrow, twisted beyond the tubercle so as to bring the inner edge up with a prominent scalene tubercle and a deep groove before and behind it. The features of the rib are sharply cut. It may be justly said that one is not justified in describing a type from two specimens; nevertheless these two specimens are among the best instances of cervical ribs. An imperfect 1st thoracic is very different. It is flat, not twisted, and without either a prominent scalene tubercle or clear grooves. It is of a more negative character. While some moderately developed cervical ribs have something of the twisted appearance of those first mentioned, others are very like the featureless imperfect 1st thoracics. It is absolutely impossible in many cases to distinguish, on an isolated specimen, between a medium-sized cervical rib and a rudimentary thoracic one. The resemblance between the cervical rib in 267 and the thoracic in 9379–38 has been mentioned; the former is rather the more like a normal 1st rib. The rudimentary 1st of A–4 and that from the left of the 7th vertebra of H–3, which is probably to be similarly interpreted, resemble each other and that of 9379–38 very closely.

---

[1] Bolk's case had not appeared. See foot-note on p. 296.

H–3 is a very interesting and perplexing case. If the ribs of the 7th vertebra are to be considered cervical, we probably have here another instance of a cervical rib of the kind found in 202, though in the absence of the sternum it cannot be certain. I incline, however, to consider them as thoracics placed too high, one of them being rudimentary. Lane (**'85**) reports an interesting case of the converse condition, in which the 8th vertebra bore on one side a rib which he considers cervical, that from the 9th being practically a normal 1st thoracic one. Lebouc (**'96–'98**) also reports two cases, considered later in another connection (p. 306), in which the 8th vertebra bears rudimentary ribs quite like cervical ones. These cases certainly point strongly to the likelihood that vertebrae of different numbers at this end of the thorax also may assume similar features. They show, moreover, how unsatisfactory the terms "cervical" and "thoracic" are in this connection.

Bicipital ribs sometimes occur and may be due to the fusion of a cervical rib with a 1st thoracic, or to the fusion of a 1st thoracic with the 2d. An instance of each is presented in 649 and in the incomplete specimen C–1, respectively. In the former the cervical rib soon joins the other, which presents no marked enlargement of its shaft, but the latter specimen shows a great broadening. Indeed it is evident that there are two ribs united even before it branches at the front into a normal 1st and 2d. Several instances of this latter condition have been described, but for the most part without conclusive data as to the number of the ribs. They have, however, a general family likeness and, moreover, one point of resemblance which perhaps has not been noted. It is the nearness of the two heads to one another. In this specimen they both rest on the 8th vertebra. This last point is very striking in all illustrations (Turner, **'83**; Lane, **'84**). While I believe that these two types are distinct, and represent what is commonly seen at different levels of the spine, I would not undertake to say that either may not be found some time at the level of the other. In this series there is one case (208) of the fusion of the three upper thoracic ribs.

I shall return to the condition of the spine as a whole in cases of cervical and defective 1st thoracic ribs.

Fusion of Atlas and Occiput. — There is no reason why this occurrence should not have the same weight in the numerical variations of the spine as fusion at other points. There are several specimens in this series which have been sufficiently described. Is this condition a return to the past (if so, to what past?), or a step towards the future?

The Fusion of the Axis and 3d Vertebra. — Fusion occurs occasionally as a pathological process, usually of advancing years, in any part of the spine. There are also certain places where it exceptionally occurs more or less frequently in the course of development, as between atlas and occiput, last lumbar and 1st sacral, last sacral and 1st coccygeal. There is another place which seems one of predilection, namely between the axis and the vertebra below it. Leboucq (**'96–'98**) has described two cases, both with imperfect ribs on the 8th vertebra, in which he thinks there is a partial reduplication of the axis, inasmuch as in certain fissures on the anterior surface he sees a repetition of the superior articular surfaces of the axis placed ventrally to the intervertebral foramina. This is the case only in his first specimen. In the second the fusion is more thorough, and the lines of separation lost. In the latter, moreover, there is an intimate fusion of the arches. I am somewhat inclined to question the accuracy of the interpretation because these fissures on the anterior surface, judging from Leboucq's drawing, do not correspond with the direction of the superior articular surfaces of the atlas. These latter slant from the middle downward and outward, while the fissures are inclined upward and outward. Moreover, in the first of my detached specimens (4767) there is on the right of the anterior surface a horizontal slit below the superior articular process of the atlas that looks at first like a repetition of it, but which, as is shown by the median section, is certainly in the axis and not beneath it. Neither in Leboucq's second case nor in any of my series is there another instance of such an appearance. In this series there are two cases of fusion of these vertebrae without any history of the rest of the column. In the complete spines there are two other cases, one certain and one perhaps somewhat doubtful. The former (264) has the bodies fused and the laminae on one side so intimately mixed as to appear as one. In 297 (26 praesacrals) the bodies are fused but apparently not mixed (if I may use the expression), but there is a fusion in the arch that points to a congenital condition. Leboucq thinks there is no doubt that there is an intercalation of the 3d vertebra, which, at least in one case, he considers a partial reduplication of the atlas. In neither of my cases is there any reason to see more than fusion. Leboucq asks whether we are to consider his finding twice an intercalated vertebra at this place anything more than a simple coincidence. He thinks that the place below the axis is a critical one in the cervical column, and that the 3d vertebra is exposed to more variations than the others. He cites Murie to the effect that the reduction of the cervical vertebrae to six in the manatus arises from an almost complete regression of the 3d. Putting aside the question of intercalation, the idea that this is a critical point receives additional confirmation from the four cases in this series.

Irregular Segmentation.—As was remarked earlier, this is much the same as inter- and excalation, but preferable; inasmuch as the latter terms too often are used to refer to a particular vertebra supposed to be added or suppressed. There are cases in this series both of the addition and of the want of a vertebra above the sacrum, in which the regions are well defined and otherwise practically normal. Two striking examples are 764 and 478. The formula of the former is C. 7, T. 13, L. 5, S. 5, C. probably 5; that of the latter is C. 7, T. 11, L. 5, S. and C. 9. In both, the cervical, lumbar and sacral regions are very nearly typical. The fact that the 1st coccygeal is fused with the sacrum in both is interesting as showing that it is probably quite an indifferent occurrence. There seems to be no other way of accounting for these spines, and for others nearly as good, but by admitting a departure from the usual segmentation.

Concomitant Variations.—Having discussed most of the variations, considered separately, we have now to consider the relation of a variation at one part of a column to a variation at another part. Allusion, indeed, has been made to the effect of a variation in one vertebra on those in the immediate neighborhood, but now we are to consider distant ones.

This brings us to the central point in the discussion of Rosenberg's theory. It has been remarked that he has admitted that it would be natural to expect some relation between the condition of the spine at one end of the thorax and that at the other, but that such a relation is not to be found. Thus if the undeveloped condition of the 1st thoracic rib is a step towards the future, it would be reasonable to expect in the same spine a corresponding advance below the thorax. Conversely, if there is an archaic condition below the thorax there should be an analagous condition above it. While there are cases that fulfil these conditions, they are quite lost in the multitude which do not, and which even present contradictory conditions at the opposite ends of the spine, being retrogressive at one end and progressive at the other.

Let us take first the ten complete spines of this series with cervical ribs (including

H–3). In no case is there an increase in number of the praesacrals, which should be expected if this were an archaic manifestation. In half the cases the number of praesacrals is normal, in three the last is partially sacralized, and in two, the most perfect cases (267 and 202), there is a praesacral too few. Turning to the literature of cervical ribs, as given by Gruber to 1869 and continued by Pilling to 1894, I find but a single case of unmistakable cervical rib with an increase in the number of praesacral vertebrae, that of Leveling (**1787**). Unfortunately in most cases the vertebral formula is not given; still in many it is reported normal, and in a few reduced. To this case should perhaps be added the two cases of Leboucq, in which there was an additional cervical vertebra with a cervical rib on the 8th, and the case reported by Lane, already mentioned. Above all there is Rosenberg's spine with 26 praesacrals and 15 ribs, the first being a cervical one. This spine, indeed, is a most satisfactory one from Rosenberg's point of view; but, admitting its authenticity, it stands alone; the overwhelming mass of observation is just the other way. Thus there are two spines, Leveling's and Rosenberg's, with cervical ribs and an increase of praesacral vertebrae not in the cervical region. On the other hand there are several instances of reduction of the number of praesacrals, and this occurs with the most perfect specimens of cervical ribs; so that while the upper part of the spine is archaic, the number of praesacrals is diminished, which is thought to be a progressive feature.

Turning now to rudimentary 1st ribs: in G–22, which is not a perfect case, as the 1st ribs are only small and not rudimentary, there is an extra thoracic vertebra; in A–4, a typical case, there is the same; in the incomplete specimen 572 there is a record of 6 lumbar vertebrae; Leboucq describes a case with one praesacral too few, and another with one too many. Here we are confronted by the fact that while the upper part of the spine shows an alleged step towards the future, the lower part shows one towards the past. Surely such a series of diametrical contradictions, both in the cases of cervical ribs and of imperfect 1st thoracic ones, is fatal to a theory, to say nothing of the difficulty of accounting for the fusion of the atlas and occiput on evolutionary grounds, and ignoring the question whether cervical ribs, if archaic, are not too archaic to be taken seriously.

It cannot be denied that it is a very serious criticism on Rosenberg's theory that a tendency at either end of the spine either to revert to the past or to stretch forward to the future may be associated with a tendency at the other of a directly opposite significance. The question then arises whether there is not some explanation that would account for both. Now in several cases in this series, and there are plenty like them in the literature, we see a tendency sometimes for the whole thorax to move forward by cervical ribs associated with absence of the last thoracic ones or with their existence in a rudimentary condition. We also see cases in which, when the cervical rib on one side is distinctly larger than its fellow, the last rib on that side is either correspondingly smaller than its fellow, or even replaced by a pretty typical transverse process; and these concomitant variations may extend even further so as to include the sacralization of one side of the last lumbar, or even the absorption of one side of the atlas into the occiput. In the same way we may have on one side the spread of the transverse processes of the lumbar vertebrae so modified that the largest (which is that of the 3d under normal circumstances) should be higher on one side than on the other, so as to be three places distant from the last rib and the more sacralized half of the last lumbar. These phenomena have been pointed out and commented on in the description of the spines, so that it is enough here to give the numbers of the spines in which they occur.[1]

Spines 1, 729, 306, H–3, have the thorax moving up practically symmetrically on both sides. A–30, 349, 202, show the movement on one, or chiefly on one, side. In G–22 there is something of a tendency for the thorax to move down. In 561 and X there is a tendency to asymmetrical shifting of several regions without the thorax being involved as a whole.

How are these things to be accounted for? As to the original cause of the variation I have not the faintest idea, but it is clear that the vertebrae at the junction of regions are particularly variable, and it seems hard to doubt that errors of segmentation may occur. The original error having occurred, there seems to be a tendency in the organism to reproduce the type as nearly as may be under the changed conditions; to make as normal a series of regions as circumstances will permit; and that this tendency manifests itself to some extent independently in the two halves of the spine. It is remarkable that the action of this tendency is not limited to the morphology of the particular vertebrae, but to some extent maintains the relative size of the several regions. The most striking example of this is in 267 in which the 11 thoracic vertebrae are so large as to make that region, judging from the bones alone, even rather longer than usual.

The Vital Principle. — Early in this paper it was stated that the vital principle was accepted as a factor in biology. Evidently I rely upon it to account both for the normal development and for the tendency to correct as much as may be the results of certain errors in development. Spine 267 is an admirable illustration. First, as to the atlas. The anterior arch is altogether wanting. Its place is supplied by two ligaments passing one from each side of the odontoid to the occipital condyle, by which the safety of the neck is secured. As this arrangement does not allow the freedom of motion of the normal articulation there is a want of union of the sides of the posterior arch, so that to a slight extent each half may move independently of the other. As even then the rotary motion is probably less than normal, the joint between the occiput and the atlas is less cup-shaped and more adapted to a sliding motion than usual. It is interesting to observe a very similar conformation in the sockets for the condyles on the atlas of H–3, which is fused with the atlas. Thus rotary motion is possible to some extent in that joint, and the work of flexion and extension was no doubt in part carried on by the other joints of the cervical vertebrae. To the action of the same cause we must turn for the modification in the length of the thoracic vertebrae, by which 11 more than compensated for the ordinary 12. In the same way is to be explained the modifications of which we have had so many examples, by which an approach to the normal dispositions of regions is so often obtained. Still another instance is furnished by spine 202, in which a cervical rib which ends free has a cartilage shooting out from the manubrium to meet it. Similar cases have been described by Lebouccq and others. This shows clearly that the production of the costal arch depends on something more than the over-development of the costal element of the vertebra. It begins at both ends in cases which approach a complete arch. Clearly there is some force acting throughout the organism, not at one point alone, to inaugurate such changes.

---

[1] The last case of rudimentary 1st rib seen at this writing, is that of Low (**1900**). There are 25 praesacral vertebrae, of which 13 are thoracic. The last rib on the side of the rudimentary 1st one is very much larger than its fellow. The last three lumbar vertebrae seem normal, except for some sacralization on one side of the last. It is on the same side as the rudimentary rib. There is an extra vertebra in the thorax.

If Rosenberg's views on the changes of position of the ilium, and the consequent modification of vertebrae according to the position it finally assumes, which we have provisionally adopted, be correct, there is the evident need of some explanation of the cause of these modifications. I can see no other than the action of the vital principle. If it be objected that this is only a name to cover our ignorance, then the objection must be made against gravitation, magnetism, etc., for in no case do we know how the force works. We see only results.

Apart from other deductions, the following conclusions seem justified.

I. Variations occur in two ways: (1) by irregular development of the costal elements at and near the ends of the regions of the spine, and (2) by irregular segmentation through which there are more or fewer vertebrae than normal.

II. Variations of both kinds are variations around a mean. It is not impossible that some of them may be reversive; that any are progressive is mere assertion.

III. Assuming the correctness of Rosenberg's studies in ontogenesis, his view may account for some of the variations, but even in these cases something more is needed to explain the concomitant changes.

IV. Variation of the costal elements at one end of a region is often associated with variation of an opposite nature of those at the other end. Several regions may be involved, and the two sides may vary independently.

V. Variations, which separately seem either reversive or progressive, generally lose that appearance when the whole spine is considered.

VI. After the occurrence of the original error in development there is a tendency for the spine to assume as nearly as possible its normal disposition and proportions. This, as do also concomitant variations and indeed all development, implies a vital principle.

I wish to express my sincere thanks to Dr. H. P. Mosher for the great care he has taken with the drawings.

The following tables are to enable the reader to find the account of any spine or incomplete specimen that may be referred to in any part of the paper.

Spine	Page	Spine	Page	Spine	Page	Incomplete specimens	Page
1	249	350	287	729	251	132	298
2	259	361	256	764	263	140	300
21	254	377	285	A–4	262	572	301
24	275	381	267	A–7	282	725–2	299
85	285	478	288	A–30	249	1392	299
110	265	492	279	A–175	259	4767	298
141	282	493	266	A–186	264	7737–3	297
202	294	504	264	A–219	281	8590	298
208	268	545	261	D–7	284	9379–37	299
257	279	561	255	G–19	247	9395–3	299
264	273	567	248	G–22	258	9638	298
267	290	578	265	H–3	276	9639	298
297	270	615	246	X	256	C–1	301
306	252	636	247	Y	266		
349	278	649	250	Z	274		

BIBLIOGRAPHY.

Albrecht, Paul.

'84. Sur les éléments morphologiques du manubrium du sternum chez les mammifères. Libre jubilaire publié par la Société de Médicine, Gand, à l'occasion du 50e anniversaire de sa fondation. P. 157.

Bateson, William.

'94. Materials for the study of variation, treated with especial regard to discontinuity in the origin of species. London. 8°. Illus.

Baur, G.

'91. On intercalation of vertebrae. Journ. of morph., vol. 4, pp. 331–336.

'97. Remarks on the question of intercalation of vertebrae. Zool. bull., vol. 1, pp. 41–55.

Bolk, Louis.

1900. Kürzere Mittheilungen aus dem anatomischen Institut zu Amsterdam. I. Ueber die Persistenz fötaler Formerscheinungen bei einem erwachsenen Manne. II. Ueber eine Wirbelsäule mit nur sechs Halswirbeln. Morph. Jahrb., vol. 29, pp. 78–93, 1 fig., pl. 4.

Dwight, Thomas.

'87. Account of two spines with cervical ribs, one of which has a vertebra suppressed, and absence of the anterior arch of the atlas. Journ. anat. physiol., vol. 21, pp. 539–550, pl. 12.

Fol, H.

'85. Sur la queue de l'embryon humain. Compt. rend. Acad. d. sc. Paris, vol. 100, pp. 1469–1472.

Fürbringer, Max.

'79. Zur Lehre von den Umbildungen der Nervenplexus. Morph. Jahrb., vol. 5, pp. 324–394, pl. 21, 22.

Gruber, Wenzel.

'69. Ueber die Halsrippen des Menschen, mit vergleichend-anatomischen Bemerkungen. Mém. Acad. Impér. d. Sc. St. Pétersb., (7), 13, no. 2, 52 pp., 2 pl.

Holl, M.

'82. Ueber die richtige Deutung der Querfortsätze der Lendenwirbel und die Entwicklung der Wirbelsäule des Menschen. Sitzungsber. Akad. Wiss. Wien, math.-nat. Cl., 85, Abth. 3, pp. 181–232, 4 pl.

Kohlbrugge, I. H. F.

'97. Der Atavismus. Utrecht.

Lane, W. Arbuthnot.

'84. Cervical and bicipital ribs in man. Guy's Hospital Rep., vol. 42 (N. S., 27), pp. 109–133.

'85. Supernumerary cervico-dorsal vertebra-bearing ribs, with vertebral and costal asymmetry ; abnormal articulation in a sternum. Journ. anat. physiol., vol. 19, pp. 266–273.

Leboucq, H.

'96–'98. Recherches sur les variations anatomiques de la première côte chez l'homme. Mém. cour. et mém. des sav. étrangers, Acad. d. Sc. Belg., vol. 55, 48 pp., 13 fig., 1 pl.

Leveling.

1787. Observationes anatomicae rariores. Norimbergae.

Low, Alexander.

1900. Description of a specimen in which there is a rudimentary first rib along with thirteen pairs of ribs and twenty-five pre-sacral vertebrae. Journ. anat. physiol., vol. 34, pp. 451–457, 3 fig.

Macalister, A.

'93. Notes on the development and variations of the atlas. Journ. anat. physiol., vol. 27, pp. 519–542.

Pilling, Erich.

'94. Ueber die Halsrippen des Menschen. Rostock. Dissertation.

Rosenberg, Emil.

'76. Ueber die Entwicklung der Wirbelsäule und das Centrale carpi des Menschen. Morph. Jahrb., vol. 1, pp. 83–197, pl. 3–5.

'99. Ueber eine primitive Form der Wirbelsäule des Menschen. Morph. Jahrb., vol. 27, pp. 1–118, 3 fig., pl. 1-5. —There is a good bibliography.

Steinbach, Erwin.

'89. Die Zahl der Caudalwirbel beim Menschen. Berlin. Dissertation.

Turner, William.

'83. Cervical ribs, and the so-called bicipital ribs in man, in relation to corresponding structures in the Cetacea. Journ. anat. physiol., vol. 17, pp. 384–400, 6 fig.

Welcker, Hermann.

'81. Die neue anatomische Anstalt zu Halle durch einen Vortrag über Wirbelsäule und Becken eingeweiht. Arch. f. Anat. Physiol., 1881, anat. Abth., pp. 161–192.

8. OBSERVATIONS ON LIVING BRACHIOPODA.

BY EDWARD S. MORSE.

(Read November 20, 1901.)

INTRODUCTION.

THE following observations on living Brachiopoda were made many years ago. My work at the outset was more in the way of a reconnaissance of the group to sustain my contention that their affinities were with the chaetopod annelids and that their molluscan affinities were remote or entirely wanting. Before the observations on Glottidia, Hemithyris and Terebratulina were put in shape for publication, I visited Japan solely for the purpose of studying the Brachiopoda of the Japanese seas, and this step led to my accepting the chair of zoölogy in the Imperial University at Tokyo. Gradually I was drawn away from my zoölogical work, into archaeological investigations, by the alluring problem of the ethnic affinities of the Japanese race. The fascinating character of Japanese art led to a study, first of the prehistoric and early pottery of the Japanese, and then to the collection and study of the fictile art of Japan. Inexorable fate finally entangled me for twenty years in a minute study of Japanese pottery. The results of this work are embodied in the Catalogue of Japanese Pottery, lately published by the Museum of Fine Arts, Boston. With this work off my hands, I turned back with eagerness to my early studies of the Brachiopoda to find that my work on Lingula and alcoholic Discinisca had been in many details anticipated by the interesting work of Joubin and the incomparable memoirs of Blochmann. In looking over my notes and memoranda, however, I find that there are many points not touched upon by these zoölogists nor by those who have worked on the more complex Testicardines, notably the otocysts, the pharyngeal glands, the accessory hearts of Hancock, the strand-like spermaries, the external glands, the pallial circulation, the life attitudes of various forms and particularly the varied and graceful movements of the brachia, and certain other features. With the assurance that some of the points will be new and that the confirmation of others will be acceptable to those interested in this fascinating group of animals, I present the contribution without further apology. It is but fair to state that, since I began this work, the staining of tissues and section cutting have become dominant in the biological laboratory. I have neither the eyes nor the leisure to acquire these new methods, but realize in a thousand ways the imperative necessity of section cutting for the proper interpretation of certain parts in the anatomy of these creatures. In this connection, however, I cannot refrain from calling attention to the opening words of an introductory lecture by Professor J. R. Thomson, the newly appointed regius professor of natural history in the University of Aberdeen, wherein he gives utterance to a note of warning as to the direction in which our biological studies are tending. He says, "Amid the undoubted and surely legitimate fascination of dissection and osteology, of section cutting and histology, of physiological chemistry and physiological physics, of embryology and fossil hunting, and the like, do we not need to be reminded sometimes that the chief end of our study is a better understanding of living creatures in their natural surroundings?" He even goes so far as to say that it is difficult to see any reason for adding aimlessly to the already overwhelming mass of morphological and systematic detail, and that what we should rather aim at, is the understanding of the chief laws of organic architecture, of the certainties and possibilities of blood-relationship among living creatures, and a true conception of what is meant by the term organization. As has been pointed out elsewhere by Professor Alfred Newton, such a warning is undoubtedly needed at the present day, when there is far too great a tendency to regard the description of mere structure as the ultimate end of biological research. "It is as if some person to whom modern telegraphy were unknown were to describe in great detail the mechanics of the various instruments employed therein, without the vaguest conception of their practical use." (Nature: July 13, 1899.)

Had Hancock been able to avail himself of section cutting he would have got no light upon the action of the oblique muscles in Lingula, or the various attitudes of the brachia, or the extreme mobility of the brachial folds or the various behaviors of the setae, the convolutions of the elongated peduncle, and many other life features. On the other hand, his elaborate system of vascular circulation with the supposed functions of the "central and accessory hearts" might have been interpreted differently had he been familiar with this modern method. It is only fair to state that my only sections were cut with a razor, without staining or supporting substance, and most of the work was done with a Tolles' triplet.

I wish here to express my obligations to Dr. C. E. Beecher, Professor W. H. Dall, and Mr. Charles Schuchert, for many favors while preparing these pages. For providing the means to meet the considerable expense involved in reproducing the many plates in lithography, I am greatly indebted to the Bache fund of the National Academy of Sciences for a liberal grant, and to Dr. Alexander Agassiz and Mr. Augustus Hemenway. Acknowledgments are also due to Mr. Meisel for the care he has exercised in making the plates.

Note of explanation. I have used the terms Testicardines and Ecardines as they are in common use, and the forms they include are well known. They parallel Owen's divisions of Arthropomata and Lyopomata, as well as those of Huxley's Articulata and Inarticulata. The names proposed by King, Gill ('73), and others also include the same divisions. As Beecher ('92) says in referring to Huxley's definitions, "these names may be conveniently retained as two divisions or sub-classes, but they fail to express the true relationships of the various groups included in them," so the terms Testicardines and Ecardines are used simply as convenient names to designate certain well known forms. In justice to Beecher, I must say here that the classification proposed by this naturalist rests on such a profound and varied comparison of the fossil as well as the recent forms that it may well be accepted as the latest and best expression of the relationships of these animals. If he were compelled to bring his four groups into two divisions, however, he would certainly group Atremata and Neotremata together, which would give us the Inarticulata, or the Ecardines, and his Protremata and Telotremata, which would give us the Articulata or Testicardines. The works of Beecher and Schuchert are above all the most painstaking and philosophical studies of these fascinating animals yet given.

In referring to *Glottidia pyramidata* I have used the generic term only, to avoid the repetition of the long specific name. In every instance, then, the word Glottidia is used for the species *pyramidata.* Judging from the well marked characters of the shell of *Glottidia albida*, a Pacific coast form, I have no doubt that the internal structure will be found to be the same as in the Atlantic coast species.

For convenience of reference I have used the term coelomic cavity without asserting that it is the true coelom. In order to be explicit, I have at other times used the terms perigastric and perivisceral cavity. I have also used the word blood to indicate the only circulating fluid I have seen in living Brachiopoda. Perivisceral fluid, periënteric fluid, chylaqueous fluid, and other terms might be more exact or perhaps less committal, but when the term blood is used it will be understood to imply the fluid, charged with various corpuscles, which is seen circulating within the tissues.

References to the plates and figures are given by numbers only; thus **49** : 3 means plate 49, figure 3. In this way is avoided the repetition of the words plate and figure, or their abbreviations.

In all cases, unless otherwise explained, the figures are drawn with their dorsal region uppermost, if seen from the front or side; and if seen from the dorsal or ventral side, the anterior region is uppermost. With two exceptions, all the figures are exact copies of my original sketches; hence many of the drawings are incomplete, some of them being mere sketch memoranda.

HABITS.

The meagreness of observations on living Brachiopoda is somewhat surprising when one considers the ease with which abundant material of certain species in life may be obtained. Without a study of the living animal it is impossible to realize the activity of the lacunal circulation, the extreme mobility of various parts of the organism, the beautiful colors of the soft parts, and the varied and graceful attitudes of the brachia.

Many of these animals may easily be kept alive; indeed, with the Ecardine forms, the vitality manifested by them is almost beyond belief. I brought home in mid-summer, from North Carolina, a distance of nearly seven hundred miles, living specimens of Glottidia. These were kept in a small food bowl. They were afterwards carried to Eastport, Maine, and then to Troy, New York, yet none of them died until late in the fall, six months after. I also brought back from Japan a number of specimens of a small species of Lingula and not one of these died until late in the year. Joubin ('86) recounts a like vitality in Crania.[1] One cannot help associating this remarkable vitality in these genera with their persistence through geological horizons from the Cambrian to the present day almost unchanged in character. Living as they do in shallow seas, the gradual elevation or subsidence of the coast-line would in no way affect their condition. Temperature alone has probably caused their disappearance from the more northern regions, but otherwise, they have survived all the mutations of geological times unchanged, and with the persistence of this vitality, they may be the last forms of life to survive on the earth as they were among the earliest preserved. On the other hand, the Testicardine brachiopods do not possess this vitality, and this group has shown an infinite diversity of form since its first appearance in geological time.

Glottidia pyramidata.[2] This sound genus established by Dall, to which I shall add further generic distinctions, was found living in great numbers on Bird Shoals, Beaufort Harbor, North Carolina. The tides in this region are very small and these shoals are exposed at low tide. For collecting these animals, as well as many other sand burrowers, I devised a large hand-dredge in the form of a dust-pan with closely perforated bottom. With this device I scooped up the sand and sifted it at the same time, often securing, at one scoop, twenty or thirty individuals. The external appearance and behavior of these small diaphanous Lingulae are so alike that when I first began the study of *Lingula lepi-*

---

[1] Joubin says "The Crania remained exposed, upon my table, to the sun, cold, heat, without being injured. Numerous algae had invaded my basins. I had left them entire months without changing their water which ought to have acquired a strong saltness. I have still the greater part of my Crania living seven months after their arrival in Roscoff and fourteen months after their gathering."

[2] I shall retain the specific name of *pyramidata* for this species until its anatomy is shown to be identical with that of *Glottidia antillarum*, which name it now bears.

dula in Japan, it was some time before I discovered that it was not even generically identical with the form now under consideration. Aside from the internal structure of the dorsal and ventral shell, the form of the protegulum, the presence of gill ampullae, the arrangement of the oblique muscles, and the more anterior position of the coelomic cavity, I found that in Glottidia the setal tubes were not formed, though the lateral setae assume a vertical position when partially buried in the sand, as in *L. lepidula*; the sand tube is much more complete and symmetrical and in alcohol is retained on the peduncle, while in *L. lepidula* the sand tube becomes detached. In general behavior, however, the two forms are almost precisely alike. Charles Schuchert ('97), in considering the enormous period in geological history occupied by the *Lingulidae*, says that the only change observable is that in the ancient forms the viscera occupy a little more and the brachia a somewhat less space than in the later forms. Glottidia by these characters is a more ancient type. This same feature in the relative space occupied by the two regions is seen in the adolescent state of Discinisca as compared with the mature state.

When an individual was placed on the sand it would slowly throw its peduncle into a series of irregular convolutions; directly the dorsal shell would be set in motion, oscillating from side to side in a peculiar rotary and sliding manner, and during this action the shells were rather close together but not entirely closed, the fringes of lateral setae were moving in a peculiar rhythm, not swinging back and forth simultaneously, but the impulse would start posteriorly and move forward; the posterior bunches of setae would swing widely back and forth; the setae, on account of their minute longitudinal markings, would appear a somewhat iridescent steel-blue. The sand by these efforts would be gathered in an irregular ridge and sometimes would adhere by the mucus which is freely emitted, so that when the animal was lifted from the water a narrow and irregular ribbon of sand would be found encircling the creature. In some cases, the posterior half of the body would be encased in a continuous sand sheath (**41**: 14). In one specimen, in which the peduncle was broken close to the body, the creature was observed to move sideways to the distance of an inch or more, piling up the sand in a ridge as it moved along (**41**: 12). It then began burying itself in the sand, going down head first, using the anterior portion of the shells in a shoveling motion and finally disappearing. The next day it was found affixed to the bottom of the bowl by the peduncular end, though not attached by the peduncle. It had made a sand case adhering to the bowl and this case enclosed the lower half of the body. Another individual traveled a distance of two inches on one side of its body, the setae plowing into the sand and forcing the body forward; other specimens penetrated the sand by means of the peduncle and, in a vermiform way, dragged the body out of sight. When at rest, the body would be half out of its burrow, the shells partially open and the lateral setae standing vertical and meeting at their tips. In no instance did I observe the fabrication of the setal tubes to be described in *L. lepidula.* The anterior margins of the pallium were thrown into folds and the anterior bundles of setae converged in a way to form rude channels for the water, which steadily flowed in and out in definite currents. The creature, though not very timid, would on certain alarms quickly jerk its body beneath the sand and out of sight. The extent of the oscillation of the dorsal shell is shown in **40**: 2. It will be seen that the right anterior corner of the dorsal shell is moved to the left so far as to cover the left anterior corner of the ventral shell. This movement is vigorous and quite rapid but not jerky. In this oscillation, the peduncular end of the shell also swings to the right and left, and the posterior adductor muscle is greatly stretched by this action. The dorsal shell oscillates from a centre near the middle of the coelomic cavity at a point about two-fifths the length of the shell, measured from the posterior end. When adhering to a plain surface, as at the bottom of a shallow dish, a wide, irregular sand tube is made, which in some cases covers the hinder part of the body (**41**: 13).

In studying Glottidia for the purpose of ascertaining its duration of life, it was observed that there was but little variation in the size of the specimens. The shells were equally fresh-looking, and there was in no instance any parasitic growth upon the shell. In an examination of a hundred individuals, no young were found. With the *Lingula lepidula* of Japan, I had precisely the same experience; the individuals appeared to be all full grown. A number of Glottidia were kept in confinement, and while showing the most remarkable vitality, as already alluded to, they all died in the fall and within a few days of one another, evidently of old age. *Lingula lepidula,* also, apparently lived its allotted span and perished in the same way. On dying, the body protrudes from its burrow and rests full length upon the sand; it gradually turns black as a result of decomposition and the slightest jar of the vessel holding it causes the body to separate from the buried peduncle and float away. An examination of the peduncle after a lapse of forty-eight hours shows the circulation of fluid within the peduncle as active as ever.

Lingula lepidula. A species of Lingula collected at Yenoshima, Japan, averaging half an inch in length, rarely exceeding this dimension, is rather doubtfully referred to *L. lepidula* of Adams. Davidson ('86–'88) supposed this form might be the young of some larger species. Adams's statement that the shell is yellowish, tinged with red (which is really the effect of the red coelomic fluid within), with the outline and dimensions given by him agrees more or less with the Yenoshima species, so for convenience of designation it will be considered as the *L. lepidula* of Adams.

The species was dredged in a few fathoms of water from a sandy bottom in a little cove on the western side of Yenoshima. The peduncle is from 2½ to 3 inches in length, the posterior third of which is encased in a sand tube of not so compact a nature as that of Glottidia, though, like Glottidia, it forms a globular ball of sand about the severed end, shorter and more bulbous, however. When the animal is placed on sand in a bowl with water, it disappears below the surface in from ten to fifteen minutes. This action is accomplished by oscillating the dorsal shell and raising and lowering the anterior margin of the shell in a kind of shoveling motion, the lateral setae in the meantime moving rhythmically back and forth, forcing the body forward and downward. If a number of individuals are placed in a bowl with sand, they soon work their peduncles to the bottom of the bowl where a number of loosely constructed burrows are made, which are firmly adherent to the bowl (**40**: 11). The individuals group themselves together in a closer cluster than do those of Glottidia. These tubes are often made in less than half a day, and in all cases the individuals had made their tubes within the space of three days. So firmly were these irregular tubes attached to the bottom of the bowl, that the sand and water could be flung out by inverting the vessel, yet they all remained dangling by their peduncles, anchored as they were by the sand tubes in which the peduncles were encased. In one experiment in which twenty-six individuals were flung upon the sand, only one attached itself with the ventral valve uppermost. In other words, those that had fallen upon the sand, ventral surface uppermost, righted themselves with this one exception. After burying its peduncle, the animal comes to the surface and projects its body a third of its length above the sand, sometimes lying nearly horizontal and at other times standing in a nearly vertical attitude. In these various positions the dorsal and ventral shells are separated anteriorly, while posteriorly the beaks of the shells are brought together as near as the peduncle will allow. The lateral setae now stand at right angles to the plane of the body, the tips of the setae meeting (**40**: 15). The setae thus form an effectual barrier against the ingress of sand in which the individual is partly buried. This barrier becomes strengthened by an accumulation of mucus upon the setae, which forms a closed partition. In the meantime the three groups of setae on the anterior margin align themselves in such a way as to form three flattened oval tubes which communicate with the pallial cavity, the central tube being slightly longest (**40**: 12, 13). The pallium is at the same time thrown into deep folds, one on each side of a median line above and below, the crests of these folds coming between the base of the tubes and in some cases almost meeting (**45**: 10). It is at precisely these points that the strong pigmentation is seen which will be referred to later as probably sensitive to light. The setae forming these tubes become coated with a film of mucus which appears to extend beyond the tips of the setae and this film is continuous with the lateral partitions just described. The function of these tubes is clearly shown when it is observed that a strong current is drawn into the lateral tubes, to be as vigorously forced out of the central tube. During this attitude the brachia have their lower surfaces turned toward the sides of the pallial chamber, while the cirri are directed inward and forward, their tips coming just at the junction of these tubes (**40**: 12). The cirri are strongly ciliated and their vigorous motions induce the currents above described.

The peculiar alignment of the lateral setae in Glottidia and *L. lepidula* will be understood when it is seen that the shells taper slightly from the posterior lateral bunches of setae, which are quite prominent toward the anterior end, while the lateral setae vary in length, being quite short posteriorly and becoming gradually longer anteriorly, so that when the dorsal and ventral shells are closed, or when the animal is in the act of crawling, it will be noticed that lines drawn along the tips of the lateral setae on each side would be parallel; now when the shells gape anteriorly and the setae meet across the gradually increasing space between the shells, the tips of the setae touch along the whole side (**40**: 15), the increasing length of the setae anteriorly balancing, so to speak, the gradual widening made by the parted shells.

On alarm, caused by the jarring of the vessel in which it is contained, or the interposing of a hand between it and the light, the animal snaps below the sand like a flash. The opening left in the sand is in shape like a transverse section of the body, with the sand piled up in a wide, shallow ridge around the opening (**40**: 10).

The animal, as might be supposed from an examination of the powerful oblique muscles, possesses considerable strength; this strength may be shown by placing upon it a heavy weight, such as the shell of a large Donax when in a short time this weight is flung off by the oscillations of the dorsal valve.

Lingula anatina. A large green Lingula, presumably *L. anatina*, was collected in numbers at the mouth of the Takahashi River, Higo, Japan, a river that empties into the Shimabara Gulf, the waters of which are so shoal that small steamers cannot approach within two miles of the shore at this point. The Lingulae were found in a gravelly and muddy deposit just beyond low tide. They were collected by drawing the fingers through the mud in rake-like fashion. The end of the peduncle was encased in a rough tube of mud an inch or more in length; in no instance was it attached to any solid substance. The blood was pinkish lake in color and, with the admixture of mucus, quite thick and dark, discoloring the water and staining the fingers in dissection. The auditory vesicles, to be described later, were plainly visible in the smaller specimens where the shells were not so opaque. The dorsal shell oscillates quite as freely and swings as far to the right and left as in *Glottidia pyramidata*, though moving less vigorously. The general behavior of the animal and the rich brown markings of the pallium and brachia were not unlike the smaller species with diaphanous shells; the ventral shell was rigidly fixed and held by the stout peduncle, which was quite firm and inelastic near the shell; the lateral setae swung back and forth, but not with that vigorous action seen in the smaller species.

SHELL.

The word shell is hardly appropriate except as a common term for all hard coverings, such as nut-shell, egg-shell, bomb-shell, and the like. The shell of the Brachiopoda in composition, structure, and relation to the soft parts has no relation whatever to the shell of the Acephala. The words scale, scutum, and elytron are equally used in widely different groups. For convenience of designation, however, the word shell will be used in reference to the outer hard parts of the Brachiopoda. It is desirable, however, that appropriate names should be given to the hardened integument of the different groups of animals supporting such coverings.

Unless the shell of Lingula be drawn from life, or from well preserved alcoholic specimens, it is, with some exceptions, impossible to get an outline of any specific value. These exceptions are the larger and heavier shells, such as those of *Lingula anatina*, wherein a heavy deposit of limy matter renders the shell more rigid, though even here a region of the shell extending in a median line from the peduncular end is generally represented a little more arched than in nature. In the diaphanous forms, such as Glottidia and the smaller species of Lingulae, the shells warp and twist quite out of shape. In one case the anterior half of the shell turned upward until the lateral edges touched in a median line. Outlines of the shell of *Lingula lepidula* drawn from life are presented at **42**: 5, while **42**: 6 represents the same shells removed from the body and allowed to dry slowly. A line below each set of figures shows the outline of the dorsal shell across the back transversely. The rounded ridge or carination, represented in the figures as running from the posterior end of the shell forward, has no existence in nature. In view of these facts it is no wonder that there is much confusion regarding the smaller and more diaphanous species of Lingula.

While the shells of *Lingulidae* collected at any one time vary but little in size, by comparing a number of specimens a series of broad and of narrow forms may be observed. These variations were so marked in *L. lepidula* that I thought the differences might be sexual. A further comparison showed that these variations blended and so the broad and narrow forms may be regarded as the extremes of variation. The extent of this variation is shown in **42**: 5. These differences were noted in *L. anatina*, *L. lepidula*, and *G. pyramidata*.

I have designated under setae, the long clusters of setae near the hinder third of the body, as the posterior cluster. The variation in the width of the shell is marked by a broadening of this region. In *L. anatina* the anterior margin is in some specimens pointed or beaked in the median line, in others it forms a rounded or flattened curve.

In examining a large number of the shells of *L. anatina* I found a certain proportion of them thickened, discolored, and eroded, forming a marked contrast to the other specimens equally large with clear green shells, thinner in texture and more perfect in condition. As all the specimens examined were collected at the same time in July, one might infer that the rougher, thicker shells belong to a last year's growth, and it is therefore possible that this species may live two or more years. In an individual of an undetermined species of Lingula, dredged in Nagasaki Bay, Japan, the dorsal shell was somewhat pointed, while the lower shell was evenly rounded in front and minutely notched in the median line (**46**: 8). This may be, however, only an individual variation.

The shell of *L. lepidula* is much more transparent than that of Glottidia and for this reason I was enabled to make out more of the internal structure, circulation, etc. In the smaller individuals the shell is steel-gray, or light bluish white; in the larger specimens a tinge of green is seen. In alcohol, these colors change to a uniform light yellowish.

In **42**: 3, a drawing is given of the peduncular end of *L. lepidula.* Here the peduncular opening is flaring and reminds one of the early brachiopods figured by Hall and others. A direct end view shows the straight, horizontal lines of accretion so often depicted in the Cambrian forms. The protegulum is oblong-ovate, the posterior margin being straight; the periphery of this stage is distinctly yellowish in color, and this is of interest as marking a distinct period in the shell growth. In the ventral shell the outlines of this early stage may often be detected in mature specimens. The dorsal shell is more pointed and shows a conspicuous, well-shouldered foramen. The successive increments of growth are seen in blunt, tumid beaks imposed one after another on the area covered by the protegulum (**42**: 3, 4, 7). In one specimen was observed a curious alation projecting on each side of the protegulum area, the result of some thickening due to the peduncular attachment (**42**: 8).

In Glottidia, the protegulum, while showing a straight posterior margin with a slight shoulder as it connects with the subsequent growth, is circular in outline; as in Discinisca, the periphery of this circular stage is minutely indented and radially striated (**42**: 2). Brooks ('78) has shown, in the free-swimming stage of this species, the same straight posterior margin with projecting points at either end. In a species of Lingula collected in Nagasaki the protegulum is ovate with the same straight posterior margin (**61**: 1). In all these instances, the peduncle is firmly adherent to the ventral shell, the beak of the dorsal shell standing free with an interspace between it and the peduncle.

In *Discinisca lamellosa*, the protegulum is elongate-ovate with anterior and posterior margins equally rounded. A perfectly circular nucleus is outlined in the posterior half of this stage (**42**: 12). This circular nucleus is made up of polygonal cells, and the irregular fracture of the edge shows that there have been no regular increments of growth. In this disk (**42**: 9), near the posterior margin, an irregular nucleus appears, surrounded by a few eccentric lines. It is an interesting fact that the successive stages of Discinisca begin with a nucleus eccentrically related to a perfectly circular stage; this circular stage, in turn, being eccentrically related to an oblong-ovate stage, which is the true protegulum; and this, in turn, being eccentrically related to an adult stage which is finally orbicular again.

The above description applies to the dorsal shell. I shall leave the relations of these stages to the early Cambrian forms to Dr. Beecher and Mr. Schuchert who have done so much to the elucidation of these interesting problems. The ventral shell does not show this circular disk, but a bi-circular outline arching inward on its posterior border. A thickened ridge runs through this stage in a median line to merge into a thickened anterior border (**42**: 13). The brachia, or rather the brachial cirri, start from the thickened, anterior border, as may be seen by referring to **61**: 9. The bi-circular outline of the ventral shell corresponds to the circular outline seen in the dorsal shell above described. A greatly magnified view of the ventral shell is shown in **42**: 10. A wide peduncular notch is formed by the rapid growth backward of the shell; on the sides of this wide notch, another growth appears with a new notch much narrower. In this figure, the beginning of the median septum appears, on each side of which a polygonal shell structure is seen. The anterior border shows three concentric outlines, and the rim is marked by irregular radiating lines. It will be seen that the long deciduous setae start from this primitive bi-circular outline (**42**: 11).

The shell of *D. stella* is quite different from that of *D. lamellosa.* When I first dredged this species at Nagasaki, I mistook it for a species of Crania. The dorsal shell is quite firm and very irregular in shape. The creature clung so closely to the rock, when first observed, that not until it erected itself on its peduncle did I become aware that it was a species of Discinisca. In *D. lamellosa* the peduncle issues very close to the posterior margin of the ventral shell, the shell substance behind the peduncle being membranous; in *D. stella* the peduncular opening is nearer the centre of the ventral shell, the dorsal shell is irregularly convex and laps considerably over the ventral shell, which is of extreme tenuity. It appears almost membranous and is so intimately blended with the ventral pallium that it must be considered an organic part of it. The shape of the ventral shell may be compared to a shallow pan with flaring rim and with the bottom pushed upwards. At **42**: 17 are shown the dorsal and ventral shells with peduncle in outline, while at 17*a* is shown the lower valve turned upside down; a series of radiating lines, some of which are branched, runs from the peduncular opening nearly to the periphery, turning up on the rim which meets the dorsal shell. These lines are somewhat irregular and clusters of fine striae occur at intervals along them (**42**: 15). The markings of the lower shell were quite unlike anything found in *D. lamellosa.* A narrow median line is seen, upon each side of which three eccentric lines spring from a nucleus, the larger curve of the eccentric being directed backward; in front of this a curved line crosses the median line and beyond this an indication of the continuation of the median line appears. This central line is the only feature seen in *D. lamellosa.*

Coecal Tubules.

A very marked characteristic of the Testicardine group is the presence, in the shell of many of them, of tubules with which the pallium has an organic connection; even the parts surrounding the peduncular foramen are supplied with them. Dr. Beecher ('92) shows that this statement is especially true with respect to the Telotremata, for in this order the deltidial covering, consisting of the deltidial plates, is secreted by the mantle border, and in punctate forms the deltidial plates are likewise punctate. On the contrary, the deltidial covering, or deltidium, in the Protremata (Thecidium, Strophomena, etc.) is primarily secreted by the peduncle and as such is always impunctate, even in the most highly punctate species, although the obliteration of the peduncle may result in a secondary punctate deposit secreted by the mantle within the delthyrium. Precisely what their functions are is still problematical. Various suppositions have been made by those who have studied these structures microscopically. It has been suggested that they might be respiratory, again it has been suggested that they were instrumental in conveying growth elements to the shell. Kowalevski ('74) is of this opinion; Schulgin ('84) is inclined to agree with him, but thinks they may have a respiratory function as well. From the glairy nature of the shells of the smaller *Lingulidae* one might suppose that in some way they functioned as mucous tubes, but in these forms only the barest traces of their existence have been detected, and in no brachiopod have these pores been seen to open externally, at least in the adult form. It was long ago established that coecal prolongations of the pallium project into these tubular perforations of the shell. In all cases, at least in the adult, a delicate periosteum covers the shell, and consequently the tubules do not communicate with the exterior. Briefly stated, these processes may be said to be aborted in the errantian forms and to be, with few exceptions, a marked characteristic of those forms which are attached by a peduncle, or of those forms in which the lower shell is welded to the substance upon which it rests. In Crania, which has no peduncle, and which is immovably attached by the lower shell, the tubules are numerously branched towards the exterior of the shell. Joubin ('86) finds that in Crania the tubules are branched in the dorsal shell only, and that they do not occur in the areas of muscular attachment. That the coecal tubules are sensory organs of some sort seems highly probable. Sollas ('86–'87) has figured a coecal tubule, in section, of *Waldheimia cranium* and shows a structure which he interprets as an organ sensitive to tactile impression. In my Embryology of Terebratulina ('73a), I compared these processes with what I regarded as an analogous structure in the test of Crustacea and considered them as organs of general sensibility. In this memoir I describe and figure in a very early stage of *T. septentrionalis*, veritable tenuous, hair-like processes, to the number of ten or more, radiating from the distal terminations of the first three tubules formed. Bemmelen ('83) suggests that I may have made a mistake in my observations of their displacement by a delicate brush. I can assure this accomplished naturalist that there was no mistake about the observation, though I agree with him that the hairs can have no relation to the radiating tubules described by King ('70). In my earlier memoir ('71) I figure and describe two short ramifications from the end of one tubule, which are probably comparable with the radiating tubules of King and probably with those of Carpenter ('56). In the early stage of Terebratulina, not only is the shell raised in a shallow collar about the external end of the tubule, but a yellowish glandular plug is seen from which radiate these delicate hairs. Claparède ('69) figures certain papillae on the elytra of Polynoë with cirri terminating in hairs, reminding one strongly of the features above described. In this connection it may be interesting to state that Davidson ('86–'88) describes a species of Crania from the Permian of England of which he says in the dorsal shell, "externally the entire surface is closely crowded by a multitude of minute, short, hollow, spinulose tubercles which produce a granulated aspect." The manner in which the ridges in Terebratulina coincide with the setae may explain the spinous character in certain forms of Productus and other fossil brachiopods; but in Crania there are no setae, and it would be an interesting inquiry as to the origin and function of these hollow, spinulose tubercles.

PEDUNCLE.

The peduncle is a characteristic feature of the Brachiopoda, though wanting in many Testicardine forms and in Crania. That the early stages of this interesting animal will show the presence of this structure, there can be no doubt. An examination of the shell of Crania shows no traces of a peduncular foramen, and it is probable that in the young stage the peduncle will be found projecting between the shells, as in the *Lingulidae*. It will be interesting to observe the attitude of the terminal end of the intestine in relation to the peduncle, for in Crania alone, among the brachiopods, the intestine terminates posteriorly and not at the side, as in Lingula and Discinisca.

The variation in the size of the peduncle and the mobility of the body upon it, is correlated with the greater or less development of the setae. In those forms in which the peduncle is prominent, as in Lingula, or endowed with special muscles, as in Discinisca, indicating great freedom of movement, the setae are excessively developed. In *D. lamellosa*, the setae form a dense fringe about the pallium. As the peduncle becomes more aborted, the setae decrease in length and become less numerous, and finally, when we come to those forms which have no peduncle, and in which the lower shell is appressed or attached to its resting place, as in Crania, Cistella, and Thecidium, the setae are entirely absent. In the young stage of Terebratulina and Hemithyris, where the body has great freedom of movement on the peduncle, the setae are very long, often exceeding the length of the shell. As these forms become larger and have less freedom of motion, the setae become shorter and are less numerous. In forms like Terebratulina, Magellania, and others, where but slight movement of the body is possible, the setae are not crowded and have no power of motion, nor do we find any muscles to animate such movement as in the *Lingulidae*. The two extremes, then, are the Brachiopoda without peduncles, attached by their ventral shells, setae absent; and the errantian Brachiopoda, *e. g.* Lingula, peduncle exceeding by several times the length of the shell, capable of vermiform contortions, and setae forming a close fringe about the periphery of the pallium and differentiated into distinct groups, capable of swinging back and forth and having the most complex muscles to effect these movements, as so beautifully depicted by Blochmann (:01).

In Lingula and Glottidia, the peduncle is firmly attached to the ventral shell just within the beak, which, in alcoholic specimens, seems to be embedded in the peduncle. The peduncle issues from the shell as a slender stalk to enlarge immediately to three or four times its diameter at its point of attachment (**54**: 1). The dorsal shell is free, and capable of an extended oscillatory, as well as a fore and aft movement; the posterior occlusor muscle is stretched to right and left as the beak of the dorsal shell swings from side to side. It is difficult to realize the extreme and varied mobility of the peduncle until one has examined Lingulae freshly dug from their burrows. For this reason I feel justified in devoting an entire plate to illustrating the various attitudes assumed by the peduncle of Glottidia in life.

I have reproduced in **40**: 5, a sketch of *G. pyramidata* which appeared on the cover of my separate on the Systematic Position of the Brachiopoda. This drawing has been repeatedly copied until all the character of the original figure has disappeared. For this reason it is here presented. Under *Habits*, the formation and character of the peduncular sand tubes have been alluded to. The *Lingulidae* thus far examined agglutinate particles of sand about the posterior end of the peduncle. The perfection of the sand or mud tube varies in the different forms studied. The formation of these tubes, more or less firm, indicates the presence of mucous glands in the peduncle, for in no other way could these sand tubes be fabricated into symmetrical and somewhat durable sheaths such as we find in Glottidia. When the animal is living in the open sand in the sea, the tube has a certain compactness and symmetry; but when confined in a shallow bowl, the animal forms a loosely constructed burrow of sand which is made adherent to the bottom of the bowl and often encloses part of the shell beside.

When the peduncle is broken, the mutilated end contracts into a bulbous form and gathers about it a globular ball of sand whose walls are much thicker than those of the normal sand tube. An injury to the peduncle of *L. lepidula* makes plain its structure. There is first a thick outer tube having little structural character, a middle tube, or sheath, having strong transverse folds on the outside, which alternate with the irregular annulations of the outer tube, and, finally, an inner tube with delicate encircling and longitudinal muscular fibres. When the peduncle is broken, the inner tube bulges like a button beyond the severed end, and in this attitude it presents a curious ribbed and turbinated appearance caused by the contraction of these two sets of muscular fibres (**43**: 1, 2). The action of the longitudinal muscles contracting in the centre, with the contraction of the outer encircling fibres, gives this button-like end the peculiar ribbed appearance shown in the figures. When only a slight contraction of the fibres takes place, the button-like end is smooth (**43**: 3). Whether the undue enlargement of the outer sheath is caused by the unnatural contraction of the inner tube or the absorption of water, I do not know.

In Glottidia the peduncle has the same structure, though I have never observed the turbinated appearance of the end. Minute transverse striae mark the surface of the peduncle, and areas of minute dots are seen which may be mucous pores, and I may add here that in life the peduncles of Lingula and Glottidia are exceedingly mucous, the mucosity extending to the body as well. The peduncle consists of a thick outer wall irregularly annulated, though this appearance is not the result of a true vermian annulation. In certain states, the peduncle in Glottidia is so symmetrically and structurally annulated that when I first saw this condition I was almost inclined to look for setae. Within this thickened tube is a lining membrane and within this is a tubular sheath held to the lining membrane by delicate connective tissue. This is shown in **43**: 6, where the body has decayed and separated from the peduncle; the inner delicate tube is seen held in place, by threads of tissue. In this figure the current is indicated running down toward the end of the peduncle and back on both sides. In **43**: 7 there seems to be a ciliated rod, on each side of which the current courses in opposite directions. On the same plate, 4, 8, 9, the current is shown running down on one side and back on the other side. In **41**: 16 is shown the appearance of the inner tube as it is drawn away from the outer sheath. A transverse section of the peduncle in alcohol shows the outer tube made up of a series of concentric layers, next a thickened cellular lining, and then a thin membrane from which spring fine fibres of connective tissue (**43**: 11). Another transverse section (**43**: 12) from a preserved specimen shows a series of folds of the inner cavity. In **43**: 5, is presented the appearance of the peduncle of Glottidia in life, and a somewhat complex structure of the parts is indicated. Thus the outer sheath, which seems almost structureless, is, at times, thrown into distinct and regular annulations; the annulations of the inner tube alternate with those of the outer tube, and the crests of these inner annulations seem to send minute processes into the outer tube. This appearance is probably due to a wrinkling of the substance. In **43**: 10 is shown a columnar epithelium on the outer surface of the middle tube; **43**: 4 shows very clearly the retraction of the inner tube, leaving a distinct space between its end and the end of the peduncle, which is enlarged and irregularly folded. The mobility of the peduncle even at its thickest portion and the manner in which the beaks of the shells impinge on its substance are illustrated by **43**: 13. The peduncle of *L. anatina* is quite opaque and but little could be seen through its walls. In Glottidia and *L. lepidula* the peduncle is somewhat translucent and the circulation of the blood within gives it a rosy hue.

A figure of the peduncle of *D. lamellosa* is given in **43**: 14. The various muscles here shown certainly indicate great mobility of the body upon its stalk.

The peduncle of Terebratulina has been most exhaustively treated by Ekman ('96), and so, for comparison only, I have ventured to give one figure illustrating the peduncle from a small specimen of *T. septentrionalis* (**43**: 15). I have shown elsewhere that in the extreme young of Terebratulina, the peduncle is elongated, exceeding the length of the shell, and with the elongated shell gives it a very linguloid appearance. In later stages it becomes shorter and sends out a number of processes which have been fully figured and described by Ekman in the memoir above referred to.

SETAE.

A very characteristic feature of the Brachiopoda is the setae which fringe the borders of the pallium. These vermian hairs arise from true setigerous follicles which are immersed at various depths in the thickened borders of the pallium. In the errantian forms they are highly mobile and act, as in the annelids, as locomotive organs; in Discinisca, they are variously barbed and in the extreme young of all forms thus far examined, the setae are not only barbed but deciduous. The setae of brachiopods differ from those of most chaetopods in not being jointed. Among the chaetopod annelids, however, there are certain sedentary forms as well as a few errantian forms in which unjointed and barbed setae are found; in Sabelliformis, for example, the setae are unjointed, hair-like, and fringed with short setellae. Sphaerodorum is exceptional among the errantian annelids in having unjointed setae; in the *Capitellidae*, also, the setae are unjointed.

In the errantian Brachiopoda, Glottidia and Lingula, as we have already seen, the setae act as locomotive organs, swinging with the same rhythmic motions that characterize the chaetopods. The setae were primarily locomotor in function and persist through inheritance, a secondary function being acquired in the *Lingulidae* in forming the lateral barriers to protect the pallial cavity from the ingress of sand and mud. In other groups, a secondary acquisition has probably been established in furnishing a nidus for diatoms and other foreign growths which they sustain, often in rich abundance, for the benefit of the animal in furnishing, or attracting, a food supply. In all brachiopods, they undoubtedly act as a sensory apparatus for tactile impressions.

The setae in all brachiopods thus far observed are marked by transverse lines, or joints, which are shouldered and which indicate successive increments of growth. Even in the almost aborted setae of Dallina the transverse lines are easily detected. Fine parallel lines also mark these hairs, and their appearance has been happily compared to the stem of an Equisetum.

In examining the setae of different genera more in detail, we shall find that in the unattached group, *Lingulidae*, they are most highly developed. Furthermore, the setae are grouped in definite clusters. On the anterior median line of the animal is a group of setae in which the middle ones are the longest, the setae on each side diminishing rapidly in length. This may be called the median cluster. The setae on each side of this cluster increase gradually or abruptly in length according to the species, becoming longest at the round angle of the shell where the anterior and lateral borders of the shell meet. These stand out at an angle from the median line of the body, right and left, and may be called the anterior clusters. From these clusters on the side, the setae very slowly diminish in length till they reach that part of the shell where it begins to taper rapidly toward the peduncular end; at this point they immediately become much longer, forming a very sharply defined cluster. These groups may be called the right and left posterior clusters. The setae between the anterior and posterior clusters may be designated as the lateral setae (**40**: 1). These clusters, with the anterior clusters, are peculiarly active when the creature is crawling over the sand or burrowing into it head foremost. Behind the posterior clusters, the setae are less numerous, and toward the peduncular end become more filiform, and are often bent and broken. They appear to be functionless and are becoming rudimentary, presenting a condition not unlike that seen in certain Testicardine forms. The proportionate length of the setae, and the outline made by the median and anterior clusters vary in the different species. In *L. anatina*, the posterior clusters are not so prominent as in *L. lepidula* and Glottidia. The lateral setae are very short, while the setae of the anterior clusters are very long, the setae rapidly increasing in length from the outside, and ending on the inner side of the cluster with the longest setae. The middle setae of the median cluster are about half the length of the longest setae of the anterior cluster, the setae becoming shorter on each side in such proportion as to form a rounded outline for the cluster (**40**: 16). In *L. lepidula* (**40**: 6) the median cluster does not assume the rounded outline seen in that of *L. anatina*; it forms a pointed cluster and the cluster is as long as, if not longer than, the anterior cluster, and this difference may be related to the tube-forming function of the setae already described and figured (**40**: 12). The anterior clusters have their longest setae in the middle of the cluster and not on their inner sides as in *L. anatina*. The clusters in Glottidia are very much like those of *L. lepidula*, except that the median cluster is much shorter than the anterior clusters. These various clusters both in Glottidia and *L. lepidula* are very prominent and sharply defined.

In Glottidia, the minute longitudinal markings of the setae remind one of the ruled gratings for spectroscopic work, and it is this feature which causes the clear steel-gray appearance and at times an iridescence when the setae are swinging back and forth.

The transverse markings of an ordinary seta number 158, and these are separated from one another the width of the seta. In *L. lepidula*, the setae are colored a light brown within the pallium, and this color extends some distance beyond the edge of the shell, as shown in **44**: 1.

After watching Glottidia and *L. lepidula* in their activities, at one time crawling slowly over the sand with the setae swinging in rhythmical motion, or when half buried in the sand, with the lateral setae standing at right angles to the edge of the shell and forming the side partitions already described, and, in the case of *L. lepidula*, forming the setal tubes, one is prepared to understand the varied functions of the complex system of muscle fibres which endow the borders of the pallium as depicted by Blochmann (:01). In the young of *Discinisca stella* the anterior setae are nearly three times as long as the diameter of the shell; the length of the setae diminishes rapidly toward the posterior end where they are very short (**61**: 3). In the mature *D. stella*, the setae are quite short and crowded together, though they are slightly longer in front than those springing from the posterior border. The setae in *D. stella* vary greatly in character; some have a brush of minute hairs, others have setellae between the joints which are more widely separated than those of Lingula, and in others still the setellae are extremely minute (**44**: 3). The setae are densely covered with various forms of minute growth. On the setae of Lingula and Glottidia, no trace of foreign growth is seen, as their functional activity prevents any adhesion of this matter. In *D. lamellosa* a rich growth of organisms abounds, and even in young Terebratulina the inactivity of the setae permits this accumulation of foreign substances. In the mature *D. lamellosa* the setae are rich light brown in color; they are closely crowded together about the entire periphery of the pallium, though not so thickly massed on the posterior border and being in this region only $\frac{1}{24}$ the length of the shell, while on the anterior border they attain the length of the shell (**49**: 2). They are mostly barbed, rarely smooth (**44**: 7). In the young of *D. lamellosa*, the setae are much longer than the diameter of the shell, becoming shorter on the posterior border or quite absent (**61**: 5, 9, 11, 12). Some are furnished with short bristles on the sides of the setae, and these setae are thicker and are not so deeply buried in the pallium as the more delicate setae which are furnished with long hair-like setellae (**44**: 9) and in rare instances more delicate setellae branching from these (**44**: 6). The setellae are bent at their junction with the setae, and those nearest the border of the pallium are bent backward. Joubin ('86) figures the setellae before they have issued from the pallium, as pointing in the same direction as the growth of the setae. This attitude would be manifestly impossible unless a sheath, enclosing the whole seta with its branches, moved outward in its growth from the follicle. On the contrary, the setellae trail backward in the growth of the seta and, after issuing from the border of the pallium, preserve for some time the bent attitude they had while immersed in the pallium (**44**: 8). Blochmann has figured their appearance correctly.

In *T. septentrionalis*, the longitudinal ribbing of the shell corresponds to the number of setae; that is to say, at the marginal termination of every rib of the shell a seta projects; this is especially marked in the early stages of the animal. In *Terebratalia coreanica*, the border of the pallial membrane is light rose-color and the setae and follicles are light yellow (**39**: 11). The setae are very short, hardly extending beyond the margin of the shell, and are embedded at various depths in the pallium. They are somewhat apart from one another (**44**: 12). In *Terebratalia minor*, the setae are extremely short and are quite widely separated from one another (**44**: 13). In *Laqueus rubellus* the setae are very short and the transverse marks upon them are much farther apart than in the other forms studied (**44**: 14). In *Hemithyris psittacea*, the setae are very short, delicate, and very brittle; the setigerous follicles are only slightly enlarged at their base. Two and even three setae apparently spring from one follicle. Between the follicles are threads of binding tissue and what appear to be muscular fibres (**44**: 15).

In summing up this brief examination of the various forms of setae here studied, it may be stated, first, that in every instance the setae are longest on the anterior border of the pallium, diminishing gradually in length around the lateral border and being shortest around the posterior border where they are tenuous, brittle, and often bent and broken;

secondly, that when in the mature form, the setae are very short; in the young of all species observed they are very long, often exceeding in length the shell (**61**), notably in Terebratulina (**61**: 16) and Hemithyris (**61**: 17).

BRACHIA.

The brachia form one of the most complex structures of the animal and, in life, one of the most beautiful. In one division they are more or less rigidly held by the calcareous loops or crura; in the other division they have the greatest freedom of movement within the pallial cavity. No drawing can convey the grace and beauty of their various motions; in one attitude suggesting the lophophore of the phylactolaematous Polyzoa, at another time thrown into a position resembling that assumed by some sabelliform worm. The attitudes of the brachia are constrained to a symmetrical position on either side of a median line in those forms having crura; even the cirri seem to be controlled by this bi-symmetrical impulse, though individual cirri often move more independently. *Hemithyris psittacea* was observed to move one coiled brachium beyond the shell in advance of the other (**46**: 14). In the *Lingulidae*, the brachia have the greatest freedom of motion, yet, so far as observed in life, the various attitudes are strictly bi-symmetrical. The veil or collar at the base of the cirri is brown, being lighter or darker in different species; the brachia are pure white, and the cirri are variously colored with brown pigmentation. The various attitudes of the brachia in *G. pyramidata* are depicted on **45**. Under a low power they present attitudes of the most exquisite grace and beauty; the brachia coil and uncoil with the greatest freedom, and sometimes the cirri stretch quite to the anterior borders of the shell and even a little beyond (**45**: 13); again the coils are depressed like a flat helix and gradually change their position, assuming the attitude of a globular helix with high spire. The axis of this helix is often changed, sometimes standing nearly vertical and then taking a nearly horizontal position, these attitudes being duplicated with perfect symmetry by the two brachia. A characteristic and beautiful attitude of the brachia of Glottidia is figured on **45**: 6. This attitude is assumed when the animal is at rest, with the anterior part of the body slightly protruding from the sand. The entire width of the pallial chamber is occupied by the out-stretched cirri. In this figure the gill ampullae may be seen projecting from the pallium above and below. The double flexure of the anterior margins of the pallium is richly colored a dark brown, and later I shall suggest that these are sensory regions susceptible to light impressions. The drawing but faintly represents the surpassing grace and beauty of the extended arms; the faint brownish tinge of the cirri, the rich brown border of the brachia contrasting with the pure white color of the remaining surface, the nearly transparent ampullae tinted a delicate rose-color by the red blood coursing through them, the deep, rich brown markings of the pallium, and the fringes of iridescent setae, form a striking picture of the beauty of these remarkable creatures. In one observation (**45**: 3) the brachia were thrown widely apart with the coils depressed; in this attitude a few cirri were seen brown in color, and these were not aligned with the other cirri but were bending irregularly. Precisely from what part of the brachia they originated, or whether they had special functions or were abnormal, was not ascertained. Similar attitudes of the brachia are assumed by *L. lepidula*, but it would be simply duplicating the figures to represent them. The veil, or collar, at the base of the cirri is a much darker brown than in Glottidia (**45**: 15; **39**: 2). In **46**: 4, the brachia of *L. lepidula* are represented devoid of cirri, and again, in **53**: 8, one brachium is shown in this way. These outlines were drawn through the nearly transparent cirri. In *L. anatina* the brachia are the purest white, the border and collar a rich dark brown. In **40**: 16, 18, is shown a view of the brachia contracted, in which the color of the borders of the brachia is represented. In young *L. anatina*, the brachia were observed extended at right angles far beyond the borders of the shell (**40**: 17).

In all my collections of *Lingulidae*, I have never met with very young or small specimens. Individuals a few millimeters in length would doubtless show a much greater freedom in the movements of the brachia. Realizing the interesting features displayed by the young of Terebratulina and Discinisca, of which it is easy to obtain examples, an important addition to our knowledge of the life attitudes of these parts will be made when the young of Glottidia and Lingula are found. It is a rather curious fact that these young stages have never, to my knowledge, been collected, and with the exception of a brief description of an early stage by McCrady and the admirable memoir by Brooks ('79), who was the first to make an important study of the swimming stages of Glottidia, nothing is known either of the embryonic or adolescent condition of these animals. In a small and unknown species of Lingula, dredged in Nagasaki Bay, and upon which but a single observation was made, the underside of the brachia was dark brown, this color extending to the mouth with widely diverging lips as well as to the cirri (**46**: 7). In *Discinisca stella*, in a young stage, the brachia, head, and neck were a rich madder brown, the dorsal cirri were dark brown, while the ventral cirri were white.

The brachia in all alcoholic *Lingulidae* are contracted to the last degree, and it is in this condition that they are always figured in memoirs on the subject. In life such an attitude is never assumed unless the shells are torn violently apart. An interesting observation will be made when *Discinisca lamellosa* is studied in life. The brachia in the preserved specimens are far more expanded and stand out more freely on each side of the prominent head than in Lingula. They are more highly endowed with muscles, not only to move the several parts, but special muscles — the retractor brachia — are found which would seem to indicate a considerable movement of the structure as a whole. It is highly probable that the brachia have the power of uncoiling and even of partially projecting from the pallial chamber. The various muscles at the base of the cirri and of the collar indicate the same mobility of parts as is found in the *Lingulidae*. In **46**: 10, is represented a section of the brachium of *D. lamellosa* at a point indicated by A, B in **49**: 2. In the sinus at the base of the brachium, which is named the small brachial sinus by Blochmann, curious little round cells occur, held together by delicate threads; their function is not known, though they may be what Blochmann terms, in this region, gland cells. At **46**: 10*a* is a greatly enlarged view of the appearance of these bodies.

In *Terebratulina septentrionalis*, three millimeters long, the cirri project slightly beyond the borders of the shell (**46**: 12). Barrett ('55) has already observed the same in the adult form. In *Terebratalia coreanica* (**46**: 13), the cirri reach quite to the inner borders of the shell but were not observed to go beyond this edge. In all those forms with crura the brachia are constrained to a more or less rigid attitude, yet there must be some elasticity in the anterior portion of the brachia.

In *Hemithyris psittacea*, the brachium forms a coil of many turns. As I have shown elsewhere ('78), the brachia are at times protruded in a coiled condition (**46**: 14). In this figure it will be seen that one coil is projected farther than the other, indicating an independent motion of the brachia. In *Hemithyris albida*, dredged in Tsugaru straits, between Yeso and Japan, the brachia were observed protruding in the same way. One individual, with the coils protruded, was suddenly immersed in alcohol and the left brachium immediately uncoiled to nearly its full length, as shown in **46**: 15. In *H. psittacea* the brachia may be partly uncoiled within the pallial chamber as shown in **46**: 16, and it would not be surprising if, under certain conditions, the brachia might uncoil and be protruded as shown in the alcoholic specimens above mentioned. The free collar about the mouth is very mobile (**46**: 17, 17*a*), and just above the mouth a white, fibrous yoke is seen connecting the base of the brachia. A rounded area which appears on each side of this yoke indicates the great sinus connecting the brachia with the coelomic cavity.

The cirri, though apparently rigid, do move with great freedom. The general appearance, as they spring in double and alternating series from the brachium, is shown in **46**: 18. The margin from which they spring is scalloped, and the cirri rise from the crests of these scallops. Scattered muscle fibres are detected running to the scalloped margin, and parallel with this margin are other bands of muscle fibres.

Cirri.

The cirri of the *Lingulidae* thus far observed are tubular to their tips and the blood circulates freely within this cavity, as shown in a cirrus of Glottidia (**46**: 2). The cirri are strongly ciliated and the ciliary movements must be vigorous to cause the rapid currents of water which steadily pass in and out of the pallial chamber (**40**: 12). The cirrus of Glottidia is marked by irregular transverse wrinkles which are repeated on the lining membrane of the cavity within, giving it the appearance of a rude sort of annulation. The walls of the cirrus are thick and the tubular cavity within has nearly the same diameter as the thickness of the wall. In *L. anatina*, the cirri are coarsely and densely ciliated.

In all Ecardine brachiopods the cirri are colored in various parts. In Glottidia, the tip of the cirrus has a light brown tinge (**39**: 7). In *L. lepidula*, it is brown on the outside from the base to a third of its length; near the tip a brown tint is seen on the inner surface (**39**: 2; **45**: 15; **46**: 5). In *L. anatina*, the sides of the cirrus are brown. The structure of the cirrus in Discinisca seems more complex than that of the *Lingulidae*. The cirri in the Testicardine group are usually white or yellowish, though Schulgin ('84) figures the cirri of *Cistella kowalevskii* as yellowish red, and these he represents as projecting slightly beyond the borders of the shell. He furthermore adds that he never saw a particle of blood enter them. The cirri of many Testicardine forms have already been figured and described, notably by Bemmelen ('83), who has, with infinite pains, given a most exhaustive series of drawings and descriptions illustrating the histology of a number of brachiopods.

At **46**: 18*a* is represented a portion of a cirrus much enlarged of *H. psittacea*. In dissection, it appears almost cartilaginous, so stiff and rigid does it seem. The ciliated epithelium is easily detached from the surface. A narrow inner tube is found in which the blood freely circulates; outside this tube is a sheath containing encircling muscle fibres, and outside of all is the firm cartilaginous-appearing substance which supports the loosely connected ciliated epithelium.

Schulgin, in the paper above referred to, described the cirrus of Cistella as having a somewhat firm exterior, which is elastic, and said that when the cirrus is bent by muscular contraction, the elasticity of this substance brings it back to position again. It has occurred to me that the cirrus of *H. psittacea* may act in the same way. There are no spiculae in the cirri, as in Terebratulina and allied forms, and though more complex in structure than the cirri of the *Lingulidae*, they bear a nearer relation to these than to those of the Testicardines. Hemithyris in other respects also approaches the Ecardine group.

Hancock ('59) states that in the brachium he found 4,000 cirri. Whether this number was based on a definite count or an estimate is not known. In the species studied in the St. Lawrence, and which has always been recognized as identical with the *H. psittacea* of Europe, I counted only 450 cirri on the brachium of a fully matured specimen. This leads me to believe that Hancock's figure is the result of a misprint and that the number should read 400 and not 4,000.

MUSCLES.

The muscles of many forms of Brachiopoda have been often figured and described, and a number of investigators have given their own interpretation of the functions of these muscles with a terminology of their own, differing, of course, from that of their predecessors. Hancock's names for the muscles of Lingula were vitiated because he argued from analogy that since the Testicardine forms had an interlocking device to prevent the lateral displacement of the shells, in Lingula, there being no such interlocking device in the shells, the muscles were so arranged as to accomplish the same purpose. He says, "Indeed the attachments of the various muscles [in Lingula] are so distributed around the margin of the perivisceral chamber that transverse, longitudinal and diagonal movements are alike guarded against. And perhaps their true functions are best understood when thus considered in co-operation; it is then seen that they form a complicated complementary system for the purpose of assisting in adducting the valves, their various points of attachment and different inclinations being so arranged, that, in whatever state of action they may happen to be, they will always keep the valves steadily and accurately opposed to each other." In commenting on the names given by previous investigators to the muscles of Lingula, Hancock says, "It is necessary to alter these later epithets as they imply what appears to be a false theory, namely: the sliding of the valves over each other." Owen ('35), to whose terminology he particularly refers and upon which he animadverts, in describing the various muscles of Lingula, says, "The arrangements of these powerful adductors are such as to effect the sliding movements of the valves on each other, beside closing the shell, and to compress and variously affect the interposed viscera and visceral lacunae with their contained sinuses," and I may add that no words could express more correctly the precise work accomplished by these muscles, for they cause not only the "transverse, longitudinal and diagonal movements" of the shell, and that in a more vigorous way than even Owen dreamed of, but they do compress and variously affect the interspersed viscera and the circulation, as will be seen farther on.

In a short paper in the American journal of science and arts in 1870, I first figured the appearance of the oscillatory and sliding movements of the dorsal valves in Glottidia, though Carl Semper ('62, '64) had described this feature eight years before. Blochmann, who has recognized this mobility of the dorsal shell, was prepared to understand the functions of the oblique muscles, and his nomenclature is so simple and so apt that I have adopted his names in this memoir. There is but little to add to what Blochmann has given of the musculature of *L. anatina*, and that is, that the anterior occlusor muscle should be recognized as containing two elements, at least, if not two distinct muscles, to which the names that he has applied to similar muscles in *Discinisca lamellosa* should be given, namely: occlusor anterior 1 and 2. He certainly shows the two elements in his figures, but calls them simply occlusor anterior. In *L. lepidula*, these two muscles vary in the appearance of the muscular bundles at their points of attachment and they vary in their color also (**47**: 6). I did not observe the separation of these muscles in Glottidia, on account of the opacity of the shell, but there is no doubt of their separation.

It remains for me to describe the muscles of Glottidia and of *L. lepidula* and to point out certain differences between them. In Glottidia, the oblique muscles are more delicate than in *L. lepidula*. The terminations of the muscles in Glottidia at their points of attachment vary slightly in color; the obliquus internus is greenish, the obliquus medius is white, while the obliquus externus is silvery in appearance. The obliquus medius has its dorsal attachment posterior to that of the obliquus internus, while in *L. lepidula*, it is anterior to that muscle. Furthermore, in Glottidia the obliquus medius passes inside of the obliquus internus, whereas in *L. lepidula* it passes outside that muscle (**48**: 1, Glottidia; 2, *L. lepidula*). The points of attachment to the ventral shell appear the same in both instances, except that in *L. lepidula* they are much nearer the posterior portion of the shell, as in *L. anatina*. In *L. lepidula*, the points of attachment of these muscles show different features in color and in the nature of the lobulated appearance, as shown in the figures (**48**: 6, 8). In *L. lepidula*, the dorsal attachment of the lateralis muscle presents features of such a character that at first I was inclined to believe that they slid back and forth to a limited extent. The dorsal terminations of these muscles present an appearance as if a thickened aponeurosis stood between them and that the muscles were attached to this and not to the dorsal shell. Vogt ('45) and Blochmann represent their appearance correctly. In Glottidia, however, they appeared to me to be attached to the shell. In *L. lepidula*, when the animal is in action, this region varies greatly, as may be seen by comparing **47**: 5 and 6. In a contracted attitude of the lateralis (**47**: 5), the oesophagus is drawn toward the stomach so as to be partly telescoped within it, and the anterior portion of the stomach appears like two horns, only a small portion of the oesophagus showing between the posterior face of the lateralis and the stomach, while the lateralis are turned sharply to the right and left respectively. The anterior occlusors are shortened in their longitudinal diameter. In **47** : 6, the lateralis muscles are drawn out, exposing a much longer section of the oesophagus and clearly exposing the pharyngeal glands, and the anterior portion of the stomach is no longer bifurcated, the anterior occlusors being also drawn out longitudinally. If these parts have a limited motion, these various appearances are accomplished mainly by a contraction of the obliquus externus, obliquus medius, and lateralis. In the contraction of the lateralis, the dorsal shell with its attachments is drawn backward, as the ventral shell is rigidly held by the peduncle, producing the appearance seen in **47** : 5, while the contraction of the obliquus externus and medius draws the dorsal shell forward, presenting the appearance shown in **47** : 6. From this description one may get an idea of the mobility of the dorsal shell.

There is but little to add to what has already been made known concerning the muscles of *D. lamellosa.* It seems strange, however, that Owen, Joubin, and others should not have seen the true character of the anterior occlusors. Blochmann is the first to give a correct figure of these muscles, in which he has shown that the occlusor muscle is really divided into two muscles, which he indicates as anterior occlusor 1 and 2. In my studies of these muscles I had intended naming them external and internal occlusors respectively, but to avoid increasing the already confusing nomenclature on the subject, I shall adopt the names given by Blochmann. In *L. lepidula*, the separation of the anterior occlusor into two elements has just been pointed out, and it would seem that they must be homologous with these muscles in *D. lamellosa.* The lateralis in Lingula and Discinisca is also found where it might be expected, considering that in Lingula the body is drawn out while in *D. lamellosa* it is concentrated. A further reference will be made to the musculature of Discinisca in a consideration of the early stages of the animal. The muscles of Terebratulina and allied forms have been thoroughly described by Hancock, and my observations are only confirmatory of what is already known. The interlocking shells of the Testicardine forms would seem to preclude any other function of the muscles save that of the opening and closing of the shells, and of causing the body to move on the peduncle. In Discinisca, the silvery and tendinous muscles connected with the peduncle imply much freedom of motion of the body. In the Testicardines the muscles have, without exception, broad bases of attachment tapering toward the middle of the muscle, while in the Ecardines, with the exception of the lateralis and the obliquus medius, the muscles have the same diameter throughout. In the young of *D. lamellosa* (**61** : 11), however, the muscles have broad bases of attachment. A very marked difference therefore is seen in the muscles of the Testicardine and Ecardine groups.

MESENTERIES AND PERIVISCERAL BANDS.

The various bands and mesenteries so characteristic of the Vermes are marked features of the Brachiopoda. These bands not only hold in place the various internal organs, but from them spring, as in many worms, the genital products. A transverse section of Glottidia, just back of the stomach, reveals a dorsal and a ventral mesentery and lateral bands springing from the intestine and attached to the various parietes. A dorsal view of the intestine of Glottidia (**50**: 8) shows the line of attachment of the dorsal mesentery running back for a short distance from the abrupt collar, which forms the posterior edge of the stomach, and then dividing to the right and left. The right line of attachment runs abruptly down the side of the intestine reaching the middle of the ventral surface (**50**: 7), and then back again and obliquely across the dorsal surface and on posteriorly. The left branch of attachment apparently continues along the left side of the intestine. These lines mark the attachment of the membrane known as the ilio-parietal band (**47**: 1). This membrane stretches across the coelomic cavity, its edges touching the oblique muscles and connecting also with the nephridia on each side and just back of the nephrostomes, sending bands to the lateral coelomic walls. It follows the upper inflection of the intestine and sends out a broad band to the posterior adductor muscle. Another sketch is given (**48**: 3), showing the appearance of the posterior bend of the intestine with a band running to the posterior adductor. A transverse section of the mid-gut presents the appearance of the ilio-parietal band, upon which may be seen delicate branches which are apparently vascular. The coelomic cavity seems to be ensheathed in a peritoneum which is attached to the dorsal parietes and seems to rest on the oesophagus and stomach and runs down on the right and left to the ventral region. A comparison with the oesophageal mesentery of Phoronis would be of interest in this connection. This membrane is quite vascular, and an injection from the peduncular cavity filled these vascular ramifications without entering the pallial sinuses or the coelomic cavity (**54**: 1, 2). Further remarks will be made on this matter under *Circulation*.

The gastro-parietal band in *L. lepidula* forms an almost complete wall between what might be called the gastric cavity and the perivisceral cavity. Its dorsal boundary is very conspicuous through the translucent shell and appears tendinous. On each side where this band joins the lateral coelomic walls, muscular fibres are seen. Blochmann observed these muscles in *L. anatina* and has called them gastro-parietal muscles (**48**: 6). In *D. lamellosa*, just back of the stomach and partially obscured by the stomachal glands, a band is attached on each side, which runs across the coelomic cavity to the right and left and terminates near the posterior dorsal face of the first anterior occlusor. This is the gastro-parietal band (**49** : 1). In alcoholic specimens this band has a marked backward flexure, due probably to the contraction of the coelomic walls. From this band, as well as from other bands, the genital products arise, to which further allusion will be made. The band is bluish white in color and is of considerable strength. When the coelomic cavity is crowded with genital products, a number of membranous strands, binding the mass together, are seen running in various directions (**49** : 2). The gastro-parietal bands are distinct enough as to their main points of attachment, and the membranous strands just alluded to appear to be proliferations from the edge of the gastro-parietal band. At **49** : 6 is shown the appearance of the intestine at the point of attachment of the gastro-parietal bands. From the posterior bend of the intestine, on the dorsal side, a band runs back connecting with the posterior wall of the coelomic cavity. This band seems to be split into several strands and is quite distinct from a genital band which appears in folds just above it (**49** : 1). Below this is a narrow band attached to the posterior bend of the intestine and connected with the coelomic walls; **49** : 3 represents a rough outline of *D. lamellosa* in longitudinal section in which attachments of these two bands are shown. In the early stages one of these bands shows very conspicuously (**50** : 15). I have called this band ilio-parietal, following Blochmann.

In *T. septentrionalis* (**56** : 2), a wide band stretches across the coelomic cavity transversely, passing over the intestine, to which it seems to be attached anteriorly, and involving the nephrostomes. Huxley compared this band with the nephrostomes suspended from it, to a landing net hanging in its frame. He was the first to call this band the ilio-parietal. From the posterior edge of this band and certainly below its edge, a narrow band arises which splits into one or more strands, and this band not only supports the "accessory hearts of Hancock," but the genital products, either ova or spermatozoa; for this reason they are called genital bands (**56** : 1, 2, 3). These bands, or at least their edges, support a strongly ciliated epithelium (**59** : 8), and during genital activity the edges become thickened by glandular growth (**56** : 2, g. g.). This same thickening of the edge of the ilio-parietal band is seen in *T. coreanica*, as will be shown in discussing the genitalia. In *T. coreanica*, the ilio-parietal band, in which the nephrostomes are involved, surrounds the stomach, becoming narrower in that part connected with the nephrostomes and sending out two narrower bands in front and laterally. Posteriorly it is connected with a median septum which runs back to the posterior coelomic wall. A strong median septum runs forward from the stomach to the anterior coelomic wall, and these two septa may be looked upon as the ventral and dorsal mesenteries respectively (**55** : 8). Other bands diverge from the stomach both laterally and posteriorly, and these are named, provisionally, ilio-parietal bands (**59** : 9).

How far these various bands are correlated in the various genera of brachiopods, it is difficult to determine. In some forms they are weakly developed, as for example in Cistella. According to Schulgin, there is no dorsal mesentery in Cistella,[1] though Kowalevski states that he has defined it. At the base of the body cavity Schulgin finds that the peritoneum forms an *excavatio peritonalis*, which plays an important part in the circulation of the blood. He also finds the inner surface of the body cavity, as well as the peritoneum, clothed with a low ciliated epithelium. Much further research will be required to ascertain the relation of the various bands and mesenteries.

ALIMENTARY TRACT.

The alimentary tract, from the mouth to the anus, is very simple. In the Testicardines it is straight with the exception of the abrupt dorsal flexure at the anterior portion, and terminates blindly. In Crania it opens posteriorly. In Discinisca it makes a simple turn to the right and opens through the lateral coelomic wall. In the *Lingulidae* it runs straight backward to the posterior wall of the coelomic cavity, then, turning to the left, it runs forward as far as the oblique muscles, to turn again, running back dorsally in line with the first segment of the intestine, and then turning to the right, terminates on the right side at a point midway between the oblique muscles and the anterior occlusor. These various lengths of the intestine are correlated with the size and extent of the coelomic cavity. In the *Lingulidae*, an elongated cavity permits the intestine to make two turns; in the less capacious cavity of Discinisca the intestine makes but one turn. In the Testicardines, where a remarkable abbreviation of the coelomic cavity is seen, the alimentary tract is concentrated into the smallest possible space; and in Crania, which has no peduncle and in which the dorsal shell is free around the entire periphery, the intestine terminates posteriorly, the only instance thus far known among living Brachiopoda. In this connection a consideration of the perforation or sometimes simply a notch in the beak of the dorsal shell of many of the fossil genera of Testicardine forms would be of interest.[2]

---

[1] Argiope of Kowalevski and Schulgin.

[2] Dr. C. E. Beecher ('92) says, "The dorsal beaks of Amphigenia, Athyris, Cleiothyris, Atrypa, and Rhynchonella are usually notched or perforate. The perforation comes from the union of the crural plates above the floor of the beak leaving a passage through to the apex. A similar opening occurs between the cardinal processes in Strophomena, Stropheodonta, and allied genera, and the chilidium may also be furrowed, as in *Leptaena* (= *Strophomena*) *rhomboidalis*. This character is evidently in no way connected with the pedicle opening, but points to the existence, in the early articulate genera, of an anal opening dorsal to the axial line, as in the recent Crania. This dorsal foramen was described and figured by King, in 1850, Hall in 1860, and by several authors since, and has commonly been termed a visceral foramen.

"Oehlert suggests that it was probably occupied by the terminal portion of the intestine. The persistence of the foramen seems to indicate an anal opening."

In the *Lingulidae*, the nutrient canal has a definite pharynx, oesophagus, stomach, and gut. In Glottidia the mouth, as seen from below, is marked by very prominent lips; these are everted, the lower lip turning backward and at times being widely distended; the upper lip showing a continuous curve, the lower lip divided by a deep median depression or thrown into four folds, as shown in **50**: 3, 4.

The lips are very sensitive and mobile, and are a continuation of the brachial fold which runs the entire length of the coiled brachia. The strong ciliary movements of the cirri sweep the microscopic organisms, upon which the animals subsist, along this groove and directly into the mouth. These parts in Glottidia and Lingula are colored brown. The mouth and pharynx stand quite free from the anterior wall, as may be seen in the various longitudinal sections figured (**47**: 2; **50**: 1, 2). The extreme mobility of the brachia and the delicate movements of the lips and brachial fold justify the belief that when the young forms are observed the mouth parts will show great freedom of motion.

A longitudinal section of the pharynx in Glottidia reveals on its upper inside surface three transverse areas of irregular depressions (**50**: 6), the ridges separating these depressions being sharp and conspicuous. This structure suggests a triturating apparatus, as the lower floor of the pharynx is smooth and the folds of the stomach and intestine are longitudinal. An external view of the dorsal portion of this region shows longitudinal muscle fibres diverging anteriorly and two distinct sets of transverse muscles which are evidently connected with the triturating surface of the pharynx (**50**: 5). The pharynx and oesophagus ascend sharply to the stomach (**47**: 2; **50**: 1, 2). The anterior portion of the stomach is globular with a slight constriction behind and then an abrupt dilatation forming a sharp collar which becomes abruptly constricted as it enters the intestine. To this collar are connected the gastro-parietal band and other membranes below, making a partition which almost separates the perigastric cavity from the perivisceral cavity. A section of the stomach of Glottidia shows the interior membrane thrown into folds. The intestine follows the same general course as in Lingula, which has been repeatedly figured; it differs from Lingula, however, in the slight flexure seen in the first length that turns forward (**47**: 1). The figure shows this portion of the intestine removed to one side in order to expose the nephridium below. The intestine within is clothed with a ciliated epithelium.

In *Lingula lepidula*, the pharynx and oesophagus are longer than in Glottidia and may be elongated or shortened by the contraction of certain muscles as already described. In a retracted state (**47**: 4), the pharynx is slightly bulging, and on each side may be seen small, round glands which occupy precisely the same position that they do in certain chaetopods. I have therefore called these bodies pharyngeal glands. They doubtless occur in all the *Lingulidae* but owing to their small size have escaped notice in preserved specimens. The oesophagus is cylindrical, slightly bulging in a contracted state, and has broad longitudinal markings due to folds within. It enters the stomach as a straight tube (**47**: 5, 6). The stomach is quite different in shape from that of Glottidia, being acutely triangular, the base of the triangle being posterior and the sides curving slightly inward. When the oesophagus is retracted, the anterior portion of the stomach projects on each side like two horns (**47**: 5). The surface of the stomach is thrown into vermiform folds and in life these folds are continually in motion, expanding and contracting (**48**: 5). The intestinal canal, as in Glottidia, is strongly ciliated.

In Glottidia the rectum perforates the lateral coelomic wall obliquely and shows a distinct projection outside, the anus being marked by six flat tubercles (**50**: 10). In *L. lepidula* the rectum enters the coelomic wall in precisely the same manner. The anus is bordered by six folds or blunt scallops like the petals of a flower, the notches between these folds continuing within the rectum as lines, due to longitudinal folds (**50**: 11). This is its appearance in life, and the parts vary in their appearance as shown in **50**: 12. The anus in Glottidia was drawn from an alcoholic specimen. In both Glottidia and *L. lepidula* it will be observed that there are six tubercles or folds, and in life the anus of Glottidia would probably present the same petal-like appearance as seen in *L. lepidula.* The faeces appear as oval pellets.

In *D. lamellosa* the head is very prominent and is probably very mobile; the mouth, as in the *Lingulidae*, is turned abruptly downward and the oesophagus runs directly upward reaching nearly to the dorsal shell, where the parts are held in place by the dorsal mesentery (**49**: 3). The stomach shows but slight enlargement; the intestine descends posteriorly toward the ventral shell and is cylindrical throughout. The anus is a mere perforation in the coelomic wall and is marked by a few radiating wrinkles (**50**: 13). In the early stages the stomach appears as a large globular cavity; a slight constriction occurs as it enters the intestine, which turns to the right and which has a slight dilatation before it enters the narrow rectum (**50**: 14, 15; **61**: 7, 10). In *D. stella*, the head is dark brown and quite prominent. In the early stages, the stomach is large and globular, nearly filling the coelomic cavity; a short intestine follows, turned abruptly to the right. The animal is represented in **61**: 2 as seen from the ventral surface.

In *T. septentrionalis*, the wide expanded lips of the mouth show great mobility in the young; the lips are thrown into one or more folds and are in continual motion. The outer layer of the intestine is composed of longitudinal muscular fibres, and when cut through, the muscular layer contracts, drawing the cut edges back as shown in **50**: 16. The faeces in spiral fusiform shape, are ejected through the mouth.

In *H. psittacea*, the alimentary tract, when divested of its attachments, assumes its natural flexures (**50**: 17). The mouth is slightly dilated; the oesophagus is long, straight, cylindrical, and marked by encircling muscular fibres, and makes an abrupt turn just before it enters the stomach which is slightly dilated. A strong peristaltic action of the oesophagus continues some hours after its separation from the body. The stomach and intestine run downward parallel to the oesophagus; the intestine continues with a slight turn forward until near the end where it turns upward and dórsally, and terminates in a blunt point. There is no bulbous enlargement at the end, as figured by Hancock, though in his specimen the end of the intestine might have been packed with excrementitious matter. The intestine is cylindrical and retains the same diameter throughout, tapering only at the end, and is brownish in color. The stomach has smooth walls. The first part of the intestine presents a glandular appearance; halfway to the end of the intestine a few spiral markings are seen, and at the end a few longitudinal markings occur. The "heart of Hancock" is a testicular knob lying back on the stomach and narrowing at its point of attachment.

Stomachal Glands.

One of the marked characteristics of all Brachiopoda is the stomachal glands, usually known as the liver. These appear, at an early stage, as simple, wide diverticula of the stomach. At the outset these folds present the color which is ever after retained. These simple folds contract and expand independently of each other, and through life the same contractility is manifested by the individual coeca making up the mass. The young stages of Discinisca, Terebratulina, and Hemithyris present these features alike. The simple fold splits into separate branches and these subdivide again and again until there is formed a great tuft-like mass of branching coeca varying in certain features in each genus, being long and tubular in Hemithyris, branching like a stag's horn in Terebratulina, and assuming the shape of blunt clusters in the *Lingulidae*. The coeca, furthermore, seem as fully charged with diatoms and other food material as the stomach itself.

Similar diverticula of the digestive tract are seen among the worms, and their function has been interpreted as hepatic. Gegenbaur ('78) throws out a word of warning in his "Elements," wherein he says, "The glandular organs connecting with the mid-gut are ordinarily regarded as hepatic, or as the 'liver'. We must be careful not to attribute anything more than the value of a convenient distinction to these names." It is well known that these glandular conditions are found in the Polyzoa, Rotatoria, and other groups; the contents of the cells are different in color and therefore, says Gegenbaur, they might rightly be considered as secreting appendages. Dr. Arnold Lang ('96) calls attention to the fact that the mid-gut diverticula are universal in the Malacostraca, and that they are comparable to the mid-gut diverticula in the Entomostraca, and remarks that these organs are generally called livers. Taking into account their physiological activity in these animals, he thinks the name hepato-pancreatic the more suitable. Joubin, in his valuable memoir on Crania and Discinisca, has been the first zoölogist, to my knowledge, to question the accepted name for these parts. He insists that they are glandular in nature and would designate them simply as stomachal glands and this name I have adopted.

In the *Lingulidae*, the stomachal glands are largely developed, branching not only from the stomach proper but from the intestine, from which is sent out a mass which occupies no inconsiderable portion of the perivisceral cavity itself. The masses springing from the stomach quite fill the perigastric cavity. The main openings into the stomach and intestine are nearly as large as the diameter of the intestine itself. In Glottidia, the terminal coeca are in the form of blunt, shallow pouches in clusters of twelve or more; the mass is very compact and greenish in color and the cavities are filled with diatoms and other food material (**51**: 1; **57**: 1). In *L. anatina* the stomachal glands appear in the form of agglomerated lobular masses, the lobules coalescing, with a whitish, membranous partition between (**51**: 2). The cavities were filled with brownish granules and the usual mass of diatoms, etc. In the *Lingulidae*, the stomachal glands form irregular-shaped masses. In *D. lamellosa*, the stomachal glands appear in the young as long coeca, closely resembling, in this respect, Terebratulina (**51**: 3, 4, 5). In preserved specimens the coeca are yellowish in color and together form a rounded compact mass (**49**: 1, 2). In *D. stella*, the separate lobules are marked by a few parallel lines again resembling the Testicardines. The mass is light amber in color, and in life the usual contractions and expansions of the individual coeca are seen (**51**: 6). In *T. septentrionalis* the stomachal glands consist of long, irregular, branching coeca, marked within by longitudinal bands which are united at the tips of the coeca and continue down into the main branches (**51**: 7, 8). In life they are in continual movement. In my Early Stages of Terebratulina, I have figured and described the development of the stomachal glands from the first outfolding of the stomach wall. In *T. coreanica* the coeca are marked by six longitudinal bands looped in pairs at the tips (**51**: 9). In *Dallina grayii*, the coeca are more slender and the bands appear looped at the tips (**51**: 13). In *H. psittacea*, the stomachal glands present an appearance quite unlike that observed in any other form studied. In the youngest individual observed, the stomachal glands of one side consisted of three short lobules, within which were irregular brownish folds in pairs, resembling the appearance of wood-graining (**51**: 10). In a more advanced stage, these coeca were marked by brown granules leaving three clear interspaces which began to assume the spiral arrangement that they finally exhibit in a conspicuous degree (**51**: 11). In the adult, they form close clusters of long coeca, the individual coecum being often slightly bent at its end. In life, a pulling-down movement of the clusters is seen at intervals. The coeca are marked by very symmetrical, closely wound spiral bands in pairs (**50**: 18; **51**: 12). In the first-named figure, the appearance is given of a portion of the stomachal glands irregularly springing from the stomach; it will be observed that the main branches are very large, as they are in Glottidia (**47**: 2). Schulgin finds a primitive form of stomachal glands in *Cistella kowalevskii*, the lobules being reduced to eight on a side. He has discovered that when the creature is well fed, the cavities of the lobules are filled with cells converging from the wall and nearly meeting in the center, and that when the animal has been kept in filtered water for several days, or otherwise starved, these cells are shriveled, and that the development of the cells is evidently for the accumulation of nourishment.

In conclusion, the stomachal glands may be regarded as extensions of the absorbent surface of the digestive tract, and are probably hepato-pancreatic in their nature. The facts that they develop as simple folds of the primitive digestive sac, that these diverticula subdivide into numerous branches, that the main branches connecting with the stomach are in some forms nearly as large as the diameter of the stomach itself, that the various coeca are filled with food material and are continually dilating and contracting, all point to the same conclusion.

SENSE ORGANS.

Among the most difficult features to make out in Brachiopoda is the nervous system. There are, of course, certain portions of this system which are always conspicuous, such as the central ganglion of Terebratalia or the oblique nerves in the *Lingulidae* and the *Discinidae*, but the ganglia about the oesophageal region and the termination of the smaller branches are certainly difficult to define. With staining and section cutting the work apparently becomes simplified. As an illustration of the obscurity of these parts, I may confess that, with all my studies of living Terebratulina, even the faintest trace of a nerve has never revealed itself to me. This fact is mentioned as an apology for the very meagre results to be presented.

The otocysts in mature *Lingula lepidula* and *anatina*, I was fortunate to make known first in a brief communication to the Boston society of natural history in 1877, afterwards published in the American journal of science and arts. In the *Lingulidae* and the *Discinidae*, a most casual examination of the coelomic cavity reveals the presence of a nerve running along the lateral walls of this cavity and terminating posteriorly. An examination of this nerve reveals at least the medullary sheath and neuraxis. In

Glottidia this nerve arises from the infra-oesophageal ganglia, runs outside of the anterior occlusor muscles, and then follows along on the inside surfaces of the oblique muscles. Hancock represents this nerve as entering and passing through the various muscles it encounters, whereas, in the three species of the family I have studied, the nerve simply passes over the surface of the muscle to which it adheres by sending out little twigs, which penetrate the muscle. At **51**: 19 is represented the appearance of these twigs branching from the main nerve. The infra-oesophageal ganglia arise just behind the brachial sinus and below the oesophagus, and the nerve passes around the anterior and lateral face of the anterior occlusor muscles. The flexures of this nerve, as shown in **51**: 14, are probably due to the contraction of the parts.

In *Lingula lepidula* the oblique nerves, one on each side of the coelomic cavity, follow in the same path and cling to the oblique muscle in the same way. Blochmann and others represent their appearance correctly. A pair of auditory vesicles is found a short distance back of the dorsal attachment of the anterior occlusor muscles and in close proximity to the inner corner of the opening of the large pallial sinus (**47**: 5, 6; **48**: 5, 6; **51**: 17, 18; **52**: 1, 2; **53**: 8, 9). In living *L. lepidula* these otocysts are very clearly defined. As the otocysts are near the dorsal surface, the separate nerves supplying them may be easily made out. These nerves originate from the infra-oesophageal ganglia. The otocyst is a clear, round vesicle, in one drawing (**51**: 18) appearing perfectly circular and containing a number of otoliths. In one otocyst twenty-five were counted. These are in constant vibration and these vibrations continue long after the parts are mutilated by dissection. The region in which the otocysts are found is a center of great activity. A number of muscles are found here, not only the termination of the great occlusors, but the gastro-parietal muscles and certain muscles that seem to control the great opening of the pallial sinus.

In *Glottidia pyramidata* the otocysts were not observed, though I am sure that, as the region in which they occur is now known, they will certainly be seen through the partially translucent shell. Professor Brooks discovered their presence in the extreme young of this species in 1878.

In alcoholic *Lingulidae* these vesicles have not been detected, though in life, when the shell is sufficiently transparent, they are easily seen. Even in *Lingula anatina*, where the shell is unusually opaque by the deposition of limy layers, I managed to find a small specimen in which the shell was sufficiently thin to make out, with great distinctness, these organs (**51**: 20). They were found in precisely the same position as described above in *L. lepidula*.

In Hancock's classical memoir, plate 61, figure 6, the dorsal aspect of the root of the oesophagus of *Magellania australis* is figured. On each side of this region and in close proximity to the nerve, a small circular body is shown which the author simply indicates as "tubercles, function unknown." It has occurred to me that these might be auditory vesicles, as they occur just where they might properly be found. If this supposition could be established, then the Testicardine as well as the Ecardine brachiopods may be considered as having auditory organs. That Glottidia and Lingula are sensitive to light there can be no doubt. They seem sensitive to the interruption of light that falls upon them and withdraw beneath the sand with a quick jerk. Any pigmentation sensitive to light, in the above genera at least, would naturally be looked for on those parts of the animal exposed above the sand, and one would expect to find these areas about the anterior portions of the pallium. Schulgin finds in Cistella an accumulation of pigmentary epithelia which at certain distances are found on the periphery of the pallium, and he is inclined to believe that these areas probably indicate rudimentary organs of sense; namely, the eyes. These parts, he says, receive nerve fibers.

In Glottidia the anterior margins of the pallium, both dorsal and ventral, are thrown into two deep and distinct folds, one on each side of a median line. The space between the folds and the shell has light brown, interrupted, and sinuous striae; the outside of this area is marked by dark brown dots, while the inner edge is marked by a dark brown stripe. The function of these folds in connection with the setal tubes has already been alluded to, but this definite pigmentation of the pallium in just the position where we might expect to find areas sensitive to light certainly suggests a function of this nature, and Blochmann has shown that a number of nerve branches run to this region in *L. anatina*; and so I venture the suggestion that these rich brown, pigmentary areas may function as sensory organs for the perception of light (**39**: 5, 6; **51**, 15, 16). *Lingula lepidula* shows precisely the same pallial folds richly pigmented. In all my drawings from life these anterior folds are seen, and I am inclined to believe that in *L. lepidula*, these folds appear only when the setal tubes are formed, and in this way, if the pigmented parts are sensitive to light, these parts are exposed at just the time when the animal is in an attitude to profit by this sensitiveness. In Glottidia, an adjustment of the setae is made, analogous to that of *L. lepidula* when it forms the setal tubes, and here again the strongly pigmented folds of the pallium become conspicuous.

In *Discinisca lamellosa*, the oblique nerves are found free in the coelomic cavity, as in the *Lingulidae*. They enter this cavity between the first anterior occlusor and the lateralis muscle. Joubin, curiously enough, does not figure this nerve. Blochmann, not only figures it, but represents it correctly as passing through the obliquus anterior and obliquus posterior muscles, but traces it no farther. He represents the posterior occlusor as being furnished with a twig from the lateral dorsal nerve, which is a peripheral nerve following the lateral wall of the coelomic cavity. My own observations show that after this nerve passes through the muscles above mentioned, it enters the posterior occlusor muscle on its inner face and there terminates in a ganglion giving off numerous twigs (**52**: 4, 5).

The marked difference between the oblique nerves of Lingula and Discinisca is seen in the fact, that, while in Lingula the nerve runs along the inner surface of the various muscles it encounters, sending twigs only to the muscular fibers within, in Discinisca the nerve not only passes directly through the muscles in its path but finally enters the posterior occlusor muscle where it terminates in the ganglionic enlargement above described.

In *D. stella*, owing to its diminutive size, but little information was secured regarding its nervous system. A central ganglion was seen on the anterior body wall below the mouth. There was no bilateral division or swelling of this central nerve; it was simply a ganglionic area from which were given off two diverging branches dorsally and two diverging ones ventrally with a median one ventrally; these were all branched (**52**: 3, 3*a*). In *T. coreanica*, an elongated oval ganglion is seen just below the mouth. This ganglion shows no bilateral division. From this ganglionic center, delicate nerves run off in bi-symmetrical arrangement to the pallium as well as laterally and ventrally (**52**: 6). The possible function of the pallial coeca as organs of tactile impression has already been alluded to.

PALLIUM.

A consideration of the pallium cannot be made without including the branchia as seen in the gill ampullae of Glottidia, the lacunal circulation, and finally a discussion of the vesicular organ recognized as the "heart of Hancock." The pallium is the principal respiratory organ, and the views of Cuvier, Vogt, and Owen were quite correct as to the nature of this highly vascular membrane.[1] Nor can we consider the pallium apart from the shell, for both hard and soft parts of this external covering belong literally to one and the same structure, and this has been recognized by students of the subject. Beyer ('86) in his interesting memoir on Glottidia, after describing in detail the structure of these parts as revealed in stained sections, says, "Their continuity renders the conclusion almost obvious, namely, that they are identical in structure; in other words the so-called horny layers of the shell of Lingula are nothing more nor less than a supporting substance." Every investigator of these parts has been baffled in an attempt to separate the shells from the lining membrane below.

---

[1] There is no reason to doubt that the brachia, and other parts where the membranes are sufficiently thin, are instrumental in the work of oxidizing the blood, though Schulgin found the cirri of Cistella closed at their point of attachment and asserts that there was no evidence of a circulation of fluid within.

In life, the pallium in the *Lingulidae* exhibits on its inner surface and around its borders a rich brown pigmentation. In the anterior portion of the pallium, this pigmentation assumes a definite color pattern. It is possible that these markings may offer characters for specific determination, though they would have to be made out from living specimens, as in alcohol these colors entirely disappear. The perfect symmetry of this pattern on each side of a median line, the rich brown color of the design in contrast to the pure white or greenish tinge of the remaining surface, with the rosy tints of the red circulating fluid in the lacunae, render the pallium a most beautiful object in life. In **52**: 8, 9, 10, 11, are given figures of the anterior portion of the pallium of *Glottidia pyramidata*, *Lingula lepidula*, *Lingula anatina*, and *Lingula* sp. (Nagasaki), respectively. The pattern of ornamentation is seen to be quite different in each form though there is some individual variation. In **39**: 1, 3, an attempt has been made to show the color of this pattern in *L. lepidula*. Reference has already been made under *Sense Organs* to the anterior folds of the pallium, which are richly pigmented and which I have surmised to be sensitive to light. The most conspicuous feature of the borders of the pallium are the crowded setae which spring from setigerous follicles somewhat deeply buried in the pallium. In **52**: 7*a*, I have indicated by a figure of Glottidia, natural size, the portion of the pallium which has been removed and of which a greatly magnified figure is given just above. In a rough way, the setae and a few rows of gill ampullae are shown, as well as the general arrangement of muscle fibers involved in the movements of the setae, so far as they could be made out with a low power. After the truly superb details of the setal muscle in *L. anatina* given by Blochmann, it seems useless to present this drawing; nevertheless an idea of the gill ampullae and setae with their general relations and color patterns are fairly portrayed, and may be of some interest.

Viewing Glottidia from the dorsal surface, a treble, gourd-like outline is distinguished, which represents the boundaries of the coelomic wall. All markings within this outline are caused by the muscles, stomachal glands, genitalia, digestive tract, etc. All markings outside this outline are made by the brachia and the sinuses and lacunae of the pallium.

The region enclosed by the dorsal and ventral pallium, fore and aft and laterally, communicates freely with the sea water. The treble, gourd-shaped figure may be defined as follows: the anterior portion embraces the region of the dorsal attachment of the lateralis muscles and the pharynx and oesophagus, and might be called the peri-oesophageal cavity; the second gourd embraces the stomach, a portion of the stomachal glands, and the first and second anterior occlusors, and may properly be designated as the perigastric cavity; the third and largest gourd, forming the main coelomic cavity, is nearly circular in shape and includes the intestine, a portion of the stomachal glands, the nephridia and genitalia, and the oblique and posterior occlusor muscles; this region may be called the perivisceral cavity. For simplicity of reference, these cavities have been mentioned under the general name of coelomic cavity. The difference between the first and second gourd-shaped outline is slight; in fact, in a comparison with a double gourd-shaped wine bottle of the Japanese, the first division might be regarded as a very wide neck to the bottle. The constriction between the second and third, or largest bulb, is not only indicated by a deep indentation but organically it is the most marked region of the three cavities, for at the junction of these two outlines are seen the gastro-parietal muscles, the otocysts, and the great openings of the main pallial sinuses.

The two broad pallial sinuses, so characteristic of all the *Lingulidae*, start from the perivisceral cavity at its junction with the perigastric cavity (**53**: 1, o. s.). The openings to these sinuses are large and narrow and stand oblique to the median line of the body; indeed they follow the outline of the perivisceral cavity above alluded to. The two main sinuses run to the anterior portion of the pallium, and, in Glottidia (**53**: 1), make a graceful outward curve at the start and then a slight inward curve. The anterior terminations of these sinuses are only one third the distance apart which separates them at their origin. On the inner side of these sinuses there start short lacunae reaching nearly to the median line and slightly inclined anteriorly. On the outer side of the sinuses there spring from nine to eleven lacunae having the same anterior inclination and reaching nearly to the base of the setae in the lateral margin of the pallium. From these lacunae there arise the gill lappets, or ampullae, the discovery of which I first announced in 1870. These number from five to eight in each lacune depending upon the length (**53**: 3). The gill ampulla nearest the median line is largest, and the others diminish in size as they approach the lateral margin. They are very transparent and the blood corpuscles may be plainly seen flowing through them (**52**: 7). Ph. François ('91), in his brief note on *L. anatina*, says, in italics, that he did not find the gill ampullae as described by me, and from the way he expresses it, indicates that he was rather inclined to question their presence in any of the *Lingulidae*. It may also be added that I failed to find them in *L. anatina*, nor were they observed in the little transparent *L. lepidula*, a species which outwardly so closely resembles Glottidia. The gill ampullae of Glottidia may well be considered another strong generic character. The folds observed by Vogt in the pallium of *L. anatina* were probably due to a contraction of the parts in alcohol. The effect of alcohol in causing the sinuses to bulge may be seen in a section of Glottidia (**47**: 3). Between these gill-bearing lacunae is a brown pigmentation which unites with the brown lateral margin of the pallium (**39**: 4; **53**: 2). The current passes outwardly along the inner side of the great pallial sinus, running into all of the inner lacunae in turn, then, reaching the anterior end of the sinus, it returns on the outer side, running into each gill-bearing lacune in turn and coursing through each gill lappet. The arrows in **53**: 1, will explain the course of this current. Nearly on a line with the anterior occlusors, are a few short lacunae which have no gill ampullae. In alcohol, as we have seen, the pallium contracts and the region of the gill ampullae is thrown into a strongly bulging fold from which the gill lappets hang and these do not appear to contract (**47**: 3). Another sinus turns directly backward from the opening of the main pallial sinus and follows along close to the lateral margin of the pallium sending a series of branching lacunae to the shallow posterior portions of the pallium. This I have indicated as the lateral pallial sinus (**53**: 1, l. p. s.). Beside the main pallial sinus and the lateral pallial sinus, there is another which turns abruptly back from the main sinus opening, runs along on each side of the gourd-shaped outline of the perivisceral cavity, inclining slightly toward the median line, and disappears in a distinct round opening near the posterior lateral border of this outline (**53**: 1, c. s.). This I have designated the coelomic sinus. It was somewhat difficult to make out the precise limits of the sinus against the dark color of the viscera within. There is seen on the dorsal side a very marked sinus running in the median line from the posterior occlusor muscle to the posterior border of the perivisceral outline. This sinus becomes filled with coloring matter when injected from the peduncular cavity. I have termed this the median sinus (**53**: 1, m. si.). Is this a trace of the dorsal vessel in annelids? The sinuses and all the lacunae, to the smallest twig, have a central ridge of ciliated epithelium which springs from that portion of the pallium next to the shell. It does not separate the sinuses and lacunae into two distinct channels or tubes. In life, the lacunae, distended by the flow of blood within, appear almost tubular, as seen in *L. lepidula* (**53**: 11, 12). There is nothing to prevent the currents, which continually flow in opposite directions, from intermixing, yet, in life, this crossing of the currents has not been observed. In **53**: 4, 5, 6, 7, are sketches of transverse sections made through the pallium, intercepting some of the smaller branching lacunae. These sections show the thickness of the pallium next to the pallial chamber, and the extreme tenuity of the membrane separating the cavities of the lacunae from the shell. That the ciliary ridges, though they separate the currents flowing in the sinus, do not separate the sinus into two tubes, may be seen in *T. coreanica*, where at certain times the sinuses are packed to repletion with eggs, and all signs of the ciliary ridges disappear; only in the terminal lacunae, in which the eggs are not found, do the ciliary ridges become apparent (**57**: 11, 11*a*). In **53**: 13, is a drawing of a portion of the lateral sinus on the right side of the posterior lobe of the pallium of Glottidia. For convenience of adjustment in the plate, the lateral margin of the pallium is horizontal, the left of the figure being posterior. By this and other figures on this plate, it will be seen how sharply defined are the sinuses and lacunae, and yet there are apparently no walls in these channels. Shipley ('83) finds the same condition in Cistella; he says, "The blood is contained in a number of vessels which run irregularly in the tissues of the body, but which chiefly lie in the mantle and that part of the body wall lining the shell. It is not possible to make out very distinct walls to these vessels which appear to be mere slits in the tissue." The pallium of *L. lepidula* shows marked differences from that of Glottidia in the disposition of the main pallial sinuses and of the smaller lacunae (**53**: 8). In *L. lepidula*, the main sinuses run nearer the lateral margins of the pallium, and their terminations are wider apart than in Glottidia; furthermore the sinus has a uniform outward curve. The lacunae, which run off to the right and left with such regularity in Glottidia, are irregular and branched. The difference is of that kind mentioned by Hancock in a species which he distinguishes as *L. affinis* in contrast to the pallium of *L. anatina*. In *L. lepidula*, the lacunae, as they branch from the great sinus, appear tubular (**53**: 11, 12). In figure 12*a* an outline of the animal, natural size, is given, with dotted line to indicate the point from which the greatly magnified drawings of the lacunae are made. The ridge of ciliated epithelium appears like an acute pyramid with apex inclined backward. On each side of the circular outline of the lacune, appear smaller sections of other structures, whether of lacunae or not, I was unable to ascertain. The courses of the currents in **53**: 8, which are indicated by arrows, are precisely the same as seen in Glottidia. My notes record no appearance of the gill ampullae. At the proximal end of the great pallial sinus is seen the opening which apparently leads to the perivisceral cavity. It is a long, narrow opening, lying oblique to the median line (**53**: 8, 9, 10). Near the inner side of this slit-like opening is seen the otocyst; small lacunae appear in the immediate vicinity but their outlines are not clearly made out. The blood pours out of this opening in a vigorous current on the inner side, runs along the inner side of the great pallial sinus, coursing through all the lacunae successively and then returns on the outer side, following up and down each lacune in turn. As the current approaches the main pallial opening, a part of the current is diverted to the outside of the lateral sinus, where it runs to the posterior end of the body to return on the inner side of the sinus, back to the main pallial opening into which it is directed. The sinuses, lacunae, and all details are symmetrically developed on each side of the median line. In **53**: 9, 10, is represented the right opening into the sinus with a portion of the right sinus as seen from the dorsal surface. The anterior wall of this opening seems to be continuous with the perivisceral wall. This opening abruptly closes at intervals, entirely checking the flow of the blood, and the corpuscles immediately dam up the entrance both inside and outside, showing that the action of the ciliary ridges is not arrested. As the openings slowly part, an impetuous rush of the corpuscles takes place, and while these remain open, the blood circulates with great rapidity (**53**: 10). This closing of the openings takes place the moment the shells begin to oscillate; the moment this oscillation ceases, the openings part and the circulation begins again. The outer side of the sinus first discharges the accumulated mass of corpuscles into the perivisceral cavity, and then the inner side of the sinus receives the outflow. The closing of these openings is always synchronous with the oscillations of the shells, and it would seem that the contraction of the oblique and other muscles involved in causing this oscillation, simply brings the dorsal and ventral shells together and the pressure thus exerted, mechanically closes the openings and checks the flow of the current. It would seem, also, that these openings are in a way controlled by definite muscles which may be seen in **52**: 1. These muscles have a thickened base of attachment and are apparently animated by a nerve which branches from the auditory nerve. These openings seem never to close, however, except when the shells are oscillating or are otherwise in movement. In my first observations of *L. lepidula*, I thought I detected a flat valve controlling the sinus opening and made a schematic drawing in section of what I conceived to be the position of this valve, but later I interpreted the behavior of these parts as above described. Blochmann, however, describes and figures a valve in *D. lamellosa* in precisely the same position as I had supposed it to exist in *L. lepidula*, though if the valve really occurred in Lingula this acute observer would certainly have discovered it. It is difficult to realize, unless one has seen it, the vigorous character of the flow of these currents. When the damming of the current takes place and a rapid accumulation of blood corpuscles piles up at the closed openings, the flood is impetuous when it starts again. The volume of this flow is so great that if any special organ was implicated in its propulsion it would easily be detected. No such organ, however, has been found.

The coelomic sinuses described in Glottidia were not so easily made out in *L. lepidula*, owing to the dark color of the organs below. There appeared in the same region, however, somewhat deeply buried, a strong ridge evidently of ciliated epithelium, which I surmised to be a ciliated ridge whose posterior end turned towards the median line and was widened and digitated, indicating a number of lacunae branching from the supposed sinus (**48**: 6, 7, v. r.).

The result of a colored injection through the peduncular cavity of Glottidia, led to an unexpected result; instead of filling the coelomic cavity and the pallial sinuses as one might naturally expect it would do, the fluid ran along each side of the posterior occlusor muscle, followed the median sinus dorsally, and then filled a vascular membrane which lined the coelomic cavity. Not a trace of the injected fluid was found in the perivisceral cavity or in the pallial sinuses. The contraction of the parts in alcohol evidently closed all the openings to these regions. Much further study is necessary to illuminate the mystery of the pallial and coelomic circulation of these animals. The injection, however, revealed the presence of a vascular sheath lining the coelomic cavity like a peritoneum.

In the peduncle of Glottidia, the inner tubular cavity shows a continuous circulation of fluid, the corpuscles coursing down the centre to the extreme end and returning on either side, probably in the deep folds which are shown in a transverse section of this part. In a peduncle in the last stages of dissolution, the blood was seen circulating as usual, though the peduncle had been for two days separated from a body black with decay. Here again is a circulation of the blood induced solely by ciliary action and not by any propellent organ.

In *L. anatina,* the shell was too opaque to observe the circulation of blood in the pallium, though the pallial sinuses and lacunae of this species have often been figured and described. The anterior border of the pallium is light brown and this color extends around the entire margin; just within this brown border, the pallium becomes the purest white and toward the centre a greenish tinge is seen. The pattern of brown pigmentation of the pallium is figured in **52**: 10. From the above observations on the circulation of the blood in the *Lingulidae,* it is certain that a propellent organ or heart is wanting in these animals.

In *D. lamellosa,* the body cavity is somewhat quadrangular in shape, occupying the posterior half of the boundaries made by the orbicular shell. It is rounded behind, dilating somewhat toward the anterior portion on a line with the stomachal glands, then narrowing in line with the anterior occlusors, which stand oblique to the median line, and terminating in front with a median depression just behind the head which projects considerably (**49**: 1). From the shoulder on each side of this anterior depression spring the anterior sinuses and on the side where the coelomic wall slightly projects, spring the lateral sinuses. The anterior sinus follows very near the median line and terminates in two slender branches. A short distance from its origin a branch turns abruptly backward and recurves upon itself; this sinus sends a number of branches toward the anterior portion of the pallium. The lateral sinus has two branches, one turning abruptly forward and the other abruptly backward. These branches supply three fourths of the pallial area with its lacunae; they divide and subdivide into minute ramifications which cover every portion of the pallium. The pallium is remarkably rich in these minute ramifying lacunae, and, so far as these were traced, the central ciliated ridge was observed in all of them. Blochmann, in his drawings, shows a narrow dark center to these ciliary ridges and in every case represents a slight interspace where they branch off from the central one, and this follows down to the minute branches. In *D. stella* the pallium is bordered with dark brown and at the base of the setigerous follicles a distinct red line is observed. At the base of the setae, which are deeply inserted, a sinus runs parallel to the pallial border. This sinus has slight swellings at uniform short intervals, and within each swelling was observed an elongated nucleus which I supposed to be a ciliary fold. The radiating pallial sinuses were not observed (**44**: 4, 5).

In *T. coreanica* (**57**: 11) the pallial membrane has a strong reddish-salmon color derived from the color of the shell. The main sinus in the dorsal pallium runs parallel to the outer lateral border of the shell and nearly midway between the outer border and the median line. It sends out twelve lacunae which subdivide once or twice before reaching the border of the pallium. The ventral pallium sends two sinuses running irregularly forward, the inner one, near the median line, sending its branches to the anterior border, the outer sinus covering the remaining surface of the pallium with a less number of branching lacunae. The two sinuses are connected with a single lacune near their origin. The terminal lacunae are shown in **57**: 11*a*, and in these may be seen the middle ridges of ciliated epithelium. The sinuses and lacunae, when filled with eggs, are dark purple in color, as shown in **39**: 14. The sinuses and lacunae in *T. transversa* seem to have the same disposition in the pallium as in *T. coreanica.*

In closing the description of the pallium I must again emphasize the fact that not only the sinuses and lacunae of the pallium support the ciliary ridges which divide and subdivide with the ramifications of the lacunae, but the minute lacunae in the nephrostome of Lingula, the papillary prominences in the nephrostome of Terebratulina, and these channels wherever seen, present the same ciliary ridges. So far as I have observed, the circulation of the blood is due to ciliary action and to the agency of this action alone; as in other groups, however, the contraction of the body must cause volumes of blood to surge back and forth.[1]

BLOOD CORPUSCLES.

In the blood of Glottidia (**54**: 3), are seen three kinds of corpuscles. These consist first: of long, oval, and fusiform bodies ranging from simple oval bodies with pointed ends to elongate forms with one or two swellings, and in a few cases showing a bifurcation at one end; these are amoeboid and bend and turn in rounding the corners of a lacune or in crowding through some narrow opening; second: small, rounded corpuscles with a constriction in the centre resembling in appearance a partially collapsed rubber ball; these are nearly uniform in size and are much smaller; third: round or oval bodies showing a slightly granulated structure and varying greatly in size; these are probably ova. The blood is rosy in color and causes the rosy hue of the pallium and peduncle. In *L. lepidula* (**54**: 4) the corpuscles resemble very closely those found in Glottidia; the elongate, fusiform bodies are more slender and without swellings; the round corpuscles have precisely the same appearance; the third kind was not present. In *L. anatina.* (**54**: 5) the blood is a pale crimson lake, or violet, in color. The various corpuscles have often been figured and described, yet it will be of interest to recall their appearance in life. The long, fusiform bodies show the processes of longitudinal division; the round corpuscles are like those of Glottidia; a few round bodies were seen with granulated structure. The filiform body seen in the figure is probably foreign. In the alcoholic *D. lamellosa* (**54**: 6) the blood contained irregularly rounded bodies tinged with brown, these had a slight depression in the centre; larger oblong oval bodies with granulated surface were ova floating in the fluid. The micropyle is shown between the two drawings. In *T. septentrionalis* (**54**: 8), a variety of irregular, apparently amoeboid particles was found in the blood; Hancock figures similar bodies as occurring in Hemithyris. From the external glands I squeezed out similar bodies; certain particles not to be distinguished from these in form were ciliated and were probably fragments of ciliated epithelium. The true blood corpuscles are exceedingly minute and I have no observations on them.

---

[1] In 1861, Macdonald, in the Transactions of the Linnean society ('61) announced the discovery "of a determinate circulation of spherical, and violet tinted corpuscles in all the ramifications of the pallial sinuses, not dependent on the contractions of the pallial cavity, but upon the undulations of a ciliary lining." This paper of Macdonald's has been singularly overlooked by English and continental workers on the subject.

In *T. coreanica*, the blood was filled with brown granulated cells of minute size, small colorless cells, and colorless granulated cells (**54**: 7).

The appearance of the corpuscular elements of the blood of the few forms of Testicardines examined was widely different from that of similar elements in the Ecardines. An examination of the blood of living *D. lamellosa* will be necessary before a comparison can be made with the blood corpuscles of the *Lingulidae*.

"Heart of Hancock."

Having described the lacunal circulation of the blood and the inducing cause of it, and the manner in which it permeates every part of the body, it remains to discuss the so-called heart of Hancock, a vesicular organ which was supposed, by Hancock, to be the true heart, and which is clearly present in most Testicardines and as clearly absent in the Ecardines. This curious little vesicle, which when present is found on the median dorsal surface of the stomach of Terebratulina, Terebratalia, Hemithyris, and other genera of the Testicardine group, is certainly an enigmatical organ. It is pyriform in Terebratulina and Hemithyris, and crenulate in Terebratalia. It is an organ very easily detected in those forms possessing it.

Hancock had discovered in 1852 that the organs which Cuvier, Owen, Vogt, and others had regarded as hearts, opened externally and were in fact oviducts. In a paper read before the British association for the advancement of science in 1856, he announced this discovery and, furthermore, stated that the true blood-propelling organ was the pyriform vesicle described by Huxley ('56) as appended to the dorsal surface of the stomach, and, until recent years, Hancock's interpretation has been the one usually accepted. Joubin ('92) finds Hancock's description of this vesicle absolutely correct in detail, the disposition of the muscular fibers alone excepted. But what Hancock mistook for arteries, Joubin designates as lymphatic lacunae and he considers the "heart of Hancock" intimately related to the digestive system, in fact an absorbent lymphatic system with a propellent heart which directs the nutrimental fluid derived from the intestine, toward the various organs of the animal. In one figure Joubin shows a series of openings which he believes connects the heart with the alimentary tract. This may be a fair interpretation of the pyriform vesicle if it can be shown to be pulsatile. The accessory "hearts of Hancock" are equally puzzling. Joubin considers these vesicles as accidental and says they are anomalous and inconstant. They certainly vary greatly in their form and appearance, as I shall show farther on, but they are not anomalous.

An organ fulfilling the functions of a heart as a propellent structure is a rhythmically pulsating organ, whether it be in the shape of a pyriform, or globular vesicle, or tubular in form. In life, it is seen to pulsate; muscle fibers to induce this pulsating behavior are found, and distinct vessels or lacunae to conduct the circulating fluid back and forth are defined. Semper ('62, '64), Lankester ('73), Shipley ('83), Schulgin ('84), Beyer ('86),[1] and others who have studied the Testicardine brachiopods alive have failed to find these conditions fulfilled by this so-called heart; on the contrary Joubin and Blochmann aver that the organ in question is pulsatile. In the Ecardine forms, where the volume of circulation is the greatest and most active, this vesicle has not been found. Neither Glottidia, Lingula, nor Discinisca reveals the presence of any vesicular organ on the dorsal side of the stomach, or anywhere along on the digestive tract, or anywhere else in the anatomy. Glandular conditions arise on the edge of the gastro- and ilio-parietal bands as well as upon the mesenteries during genital activity and if this growth takes place on the dorsal mesentery, it might easily be mistaken for the so-called heart. I have examined with the greatest care many living Terebratulina and numbers of the large *Terebratalia coreanica*, *Dallina grayii*, and *Hemithyris psittacea*, solely for the purpose of studying this problem. I have opened individuals quickly, yet with great care, and have never seen the slightest signs of contractility or change of form either in the central or accessory organs denominated as hearts, nor could these vesicles be made to contract by the application of external stimuli, such as pricking with a needle. This is all the more singular, since all other parts of the organism are in constant movement. No matter how rudely the shells were torn apart (and in this operation almost the only parts that were not ruptured by this mutilation were the intestine and the dorsal vesicle) the various movements of the parts have continued for hours after this rough treatment. The various lobules of the stomachal glands are incessantly expanding and contracting, the stomach and oesophagus exhibit peristaltic and other movements hours after excision, the lips of the mouth and the delicate brachial fold at the base of the cirri continue to bend and wave, the cirri are continually turning and swaying in various directions, the circulation of blood goes on actively in the sinuses and lacunae of the pallium and in other parts, and an equally active circulation is seen in the tubular cavity of the peduncle, even days after its separation from the body black with decay, and yet the so-called heart gives no sign of contraction. It may be said without exaggeration that the only part of the anatomy which manifests no movement, which is absolutely inert, is the so-called heart. As to the well defined veins which Hancock describes in the pallial sinuses and lacunae, we have seen that they are ciliary ridges which continue into the minutest ramifications.

---

[1] Carl Semper, in a review of a previous account of his on living Lingula, says, "In spite of the desire to verify by researches on the living animal the statements of Huxley and Hancock which seem to be most exact, I could only convince myself of the correctness of my representations formerly published which to be sure, I can improve in unimportant details, but on the whole must remain as found then. In vain have I searched for that which Huxley is pleased to call the heart."

Lankester says in regard to *Terebratula vitrea*, "I entirely failed to convince myself that the organ regarded by Mr. Hancock as a heart really has the function of one in *T. vitrea*. I repeatedly opened fresh specimens with rapidity, in order to witness its contractions, if any, but never saw such contractions; nor could I find vessels in connection with it, nor evidence that it had muscular walls. Dr. Krohn, of Bonn, had equally been unable to obtain evidence that this curious little dilatation has the function of a heart."

Shipley in his studies of Cistella says, "Like other recent observers I have been unable to find anything corresponding to a central circulatory organ, or to the system of arteries and accessory pulsatile organs described by Hancock."

Schulgin, writing of Cistella says, "The particles of blood are kept in circulation by the ciliated epithelium. Argiope [= Cistella] is, therefore, devoid of a heart and of a closed vascular system."

Joubin, in his study of Crania says, "There is no trace of the existence of a heart or arterial system. All the organs are bathed in the colorless liquid filling the perivisceral cavity."

Beyer says, in regard to *Glottidia pyramidata*, "Our own observations have been only confirmatory of the views held by Shipley, Schulgin and Morse, and the most careful search after the central propelling organ over the posterior slope of the stomach invariably proved unsuccessful in every new series of transverse sections which was made."

In any discussion as to whether the " heart of Hancock " is really a propellent organ and implicated in the circulation of the blood, two matters must be considered: first, that the Brachiopoda are remarkably alike in all leading structural details, and for this reason it is difficult to conceive of so fundamental a structure as a pulsating heart being present in one group and not even a vestige of it to be found in another group; second, one has only to realize the active and abundant flow of blood in the perivisceral and pallial circulation, to be convinced of the utterly inadequate character of the little pyriform vesicle to induce such a flow, and when one turns to Glottidia and Lingula and witnesses the voluminous and impetuous flow of blood through the sinuses and yet finds no trace of a heart or a pulsating organ to induce this current, he is compelled to find some other explanation for the function of this vesicle in the Testicardines.

Another question must be asked: are the central and accessory vesicles related organically? They certainly appear to have a similar structure. In *T. coreanica* the curious lamellated central organ, the so-called heart, is connected with the lateral vesicles through a colored and glandular thickening of the edge of the ilio-parietal band. Now this thickening is, I believe, associated with genital activity, and later I shall show that the immediate region of the accessory hearts becomes changed during genital activity and a number of glandular prominences make their appearance on the genital band at this time. The central and accessory hearts appear so identical in structure and color that it would seem they were related functionally. I shall discuss the accessory "hearts of Hancock" under genitalia, but must remark here that these hearts appear in every case in close proximity to the nephrostomes, and as these in the Testicardines appear at the coelomic termination of the great pallial sinuses, the accessory hearts are found also in close proximity to these terminations. Hancock represents them in *Magellania flavescens* as attached to a band, the end of which is actually imbedded in the termination of the pallial sinus. I have not observed this condition in associated forms. Hancock also represents in *M. flavescens*, four accessory vesicles, two dorsal and two ventral, corresponding to the pallial sinuses, yet in this species there are only two nephridia. In *H. psittacea*, there are four nephridia and also four accessory vesicles. In *T. septentrionalis* there are four pallial sinuses, yet only two accessory vesicles. It is somewhat singular that a careful study of Lingula, Glottidia, and Discinisca failed to reveal the presence of any organ corresponding to the "heart of Hancock" or to the accessory hearts, though the nephridia are conspicuous organs, as they are in all brachiopods; on the other hand there is no feature more constant than the pallial sinuses, yet with this constancy in structure we find the "heart of Hancock" and the accessory heart, with few exceptions in the Testicardines only. In other words, in those brachiopods in which the coelomic cavity is contracted to the smallest space and the greater mass of the genitalia arise in the pallial sinuses, the central and accessory vesicles are present, while in the Ecardine forms, in which the coelomic cavity is capacious and the genitalia are confined to this cavity alone, these vesicles are absent. I think, therefore, that the accessory vesicles at least, may with reason be considered under genitalia and not under the circulatory apparatus.

NEPHRIDIA.

The paired oviducts in Brachiopoda are so identical in form, attachment, and function with similar organs in the chaetopod worms that I formerly designated them segmental organs from the name first given by Williams ('51), to the oviducts of annelids.

This name was adopted by Claparède in his remarkable researches on the annelids of the Bay of Naples. So absolutely identical are these organs in details of structure, attachments within, their associated parts and external openings, with those of certain chaetopod worms that the description of these parts might be taken from Claparède with hardly the alteration of a single word. The wide divergence in the form of these organs in worms is, with the exception of the length and convolution of the tube, paralleled in the Brachiopoda, as may be seen by an examination of the figures given in plates **54**, **55**, **56**. Gegenbaur ('78) properly objected to the name segmental organs as other organs and parts are repeated segmentally. There is, however, no end of inappropriate names for organs and groups in the animal kingdom. What more ridiculous than the name Mollusca or more preposterous than the name Brachiopoda as applied by Cuvier, based on false homologies. Nevertheless as these organs are now recognized under the name nephridia in worms and other divisions of the animal kingdom, it is well to apply the same name to these parts in the Brachiopoda. It is not yet established that these parts are renal in their nature. One thing, however, is certain and that is, that they are plainly oviducts, and this would be a far more appropriate name for them.

In a general way, it may be stated that, with the exception of Hemithyris which has two pairs of nephridia, the genera thus far observed have but a single pair. In the *Lingulidae*, the nephridia are quite constant in their form and position, while those of Discinisca and Crania are quite different in form. Among the Testicardines, the nephridia vary greatly in the different genera. In *T. coreanica*, the tube is abruptly bent upon itself. In *T. septentrionalis*, the nephrostome stands at a slight angle from the tube. In *Dallina grayii*, the nephrostomes are close together and the tubes are straight, the nephrostome much exceeding, in diameter, the tube. In Hemithyris, the nephridia are quite wide apart, and the tube is short, and wider in diameter than the nephrostome. In all, however, the nephrostome is crenulated and strongly ciliated, and in all, with the exception of Discinisca and Crania, a more or less sharp constriction separates the nephrostome from the body of the nephridium, and in all, with the exception of Discinisca, the body of the nephridium is thickened, glandular and has a pronounced color. In Glottidia, it is a rich dark orange; in *L. anatina*, it is marked by dark, maroon lines; in Terebratulina, it is a yellowish brown; in *Dallina grayii*, it is a rich, rose color streaked with darker areas.

The position of the nephridia in the *Lingulidae* has been so well defined by authors that it is only necessary to call attention to their appearance in life. In Glottidia (**54**; 9), the body of the nephridium lies parallel to the lateral body wall, the central axis of the nephrostome standing at nearly right angles to the longitudinal axis of the organ. The nephrostome is turned closely to the body wall. It is rather deep, slightly flaring at the rim and foliated within. It is held firmly to the body wall by the ilio-parietal band (**47**: 1). This band is divided into several strands, one of which, rather wide, passes directly behind the nephrostome and is attached to the body wall; another, very narrow, passes obliquely backward to the body wall, and still another, a very narrow one, passes obliquely backward toward the median line. The appearance of the inner portion of the nephrostome is shown in **54**: 10. The blood in active circulation is seen rushing through the various lacunae which cover the surface of the nephrostome. The whole organ is highly vascular throughout and it would seem that the endothelial lining of the coelomic cavity ensheathed every organ within. The body of the nephridium is a rich orange color, and in *L. lepidula* the color is so persistent that after a lapse of twenty years, in alcohol, the color through the shell appears just as bright. The body of the nephridium in Glottidia has an oblong, slightly ovate form, narrowing quite rapidly to its outer termination; it has a few wide longitudinal markings which probably indicate folds within. In *L. lepidula* (**54**: 11, 12, 13), the nephridia occupy precisely the same position as in Glottidia. The nephrostome is somewhat different; in shape it is like a cup with the rim sharply reflected, and just below the rim a deep constriction, and then the wall rounds out again to taper rapidly to the body of the nephridium which it joins at nearly right angles to its axis (**48**: 4, 8). The side of the nephrostome next to the coelomic wall is so closely adherent to it that the wall itself forms part of the border of the nephrostome (see particularly, **54**: 12, 13). In Glottidia and *L. anatina*, the rim of the nephrostome is entire, while in *L. lepidula* the rim merges with the body wall. The folds within the nephrostome (**54**: 14, 14*a*) are in the form of loops giving the appearance of a deep fluting. The folds are strongly ciliated and the ciliary action is vigorous. No current was seen to pass through the nephridium; corpuscles were drawn into the nephrostome only to be whirled out again. Here is an evidence that in some way the animal controls the discharge of matter through it. In Terebratulina, I have followed an egg from its release from the pallial sinus to its entrance into the nephrostome and final discharge at the exterior opening (**58**: 4). There are a few branching lacunae on the walls of the nephridium which is a rich, dark orange, and the color is so pronounced as to show through the shells. The tube follows along the side of the coelomic wall and passing through it obliquely, opens on the anterior wall. The external openings appear as simple slits (**48**: 4, 8). The nephridia of *L. anatina* are not unlike those of Glottidia. The body is thick, wide, flattened, and glandular; the nephrostomes seem a little more closely appressed to the coelomic wall and the folds converge slightly to the anterior end, as such lines would on an oblong and tapering body. The folds are finer and run parallel to the inner incurving outline of the nephridium. These folds are a rich maroon color. A reference to **55**: 1 will better explain these features. The nephrostome is not so deep as in Glottidia or in *L. lepidula* but is more flaring and the rim is slightly undulating. The body of the nephridium is held to the perivisceral wall by a narrow band immediately behind the obliquus internus, and this may be a continuation of the ilio-parietal band. A greatly enlarged view of the nephrostome and a portion of the nephridium is given in **55**: 2. It is seen to be highly vascular; large branching lacunae run from the base of the nephrostome to the periphery; these divide, and just before reaching the rim they appear, in the drawing, to be recurved. This appearance is due to the incurving edge of the flaring rim which is very thin and transparent. The lacunae have a delicate light brown tint. The ciliated ridge is seen running in the centre of each lacune and the blood follows up and down the branches, the current being divided by this ridge. In the undetermined species of Lingula, the nephrostomes were turned toward the perivisceral cavity (**40**: 18). Whether during genital activity the nephrostome has the power of turning in this way, is not known. In *D. lamellosa* (**55**: 3) the nephridium, while occupying a position similar to that in the *Lingulidae*, is quite different in its attitude. The nephrostome is turned towards the coelomic cavity and obliquely toward the dorsal shell. It is wide and flaring with regular radiating folds running from the inside nearly to the periphery. It is held to the lateral body wall by a band which seems continuous with the membrane composing the nephrostome. This flaring mouth connects at once with the tubular portion of the nephridium without the usual constriction seen in the nephridia of other forms and there is no glandular enlargement or thickening. The tube tapers gradually to its termination in the anterior wall of the coelomic cavity. These openings are seen externally just below the mouth on each side and about midway between the dorsal and ventral parietes. The external openings stand oblique and incline to each other (**55**: 4). A view from within this wall shows that the tubes follow along the ventral floor of the coelomic cavity and then turn upward along the body wall, piercing the wall obliquely (**55**: 5). Externally the openings are as simple as in *L. lepidula.* In the early stages of *D. lamellosa*, the nephridium has a long, narrow nephrostome suggesting somewhat the appearance of the same part in Crania as figured by Joubin, though his figure represents the nephrostome as bifurcated. The edge appears to be minutely fringed and the tube shows a slight enlargement in its course (**55**: 6). The small circle associated with the figure indicates the size of the specimen from which the nephridium was drawn.

We have seen in the *Lingulidae* a constancy in form and position of the nephridia quite in accordance with those resemblances in structure seen in all the parts. In Discinisca, the nephridia are quite unlike those of the *Lingulidae*, as is the animal itself. Crania stands quite apart from all in the form of this organ. In the Testicardine Brachiopoda, the nephridia vary from one another quite as much as does the internal structure of the different forms, or the external appearance of their shells.

In *T. septentrionalis*, the nephridia are suspended from the gastro-parietal band on each side of the intestine, with the nephrostomes opening toward the dorsal shell (**56**: 2). This figure represents the right nephridium with a portion of the intestine and the divaricator muscles. The band, by which the nephrostomes are held, stretches across the coelomic chamber and adheres to the intestine as well. In **56**: 1, is shown the left nephridium in profile. The nephrostome is wide, and within, the surface is thrown into a number of irregular folds which on one side gradually merge into papillae. Two of these are shown more highly magnified, within which may be seen the ciliary ridge (**56**: 2*a*). The agaric-like regularity of these folds, as figured by Hancock, in *T. caput-serpentis*, is not observed in *T. septentrionalis*, at least in its living state, and I may add also that Hancock represents the nephrostomes as quite close together, while in *T. septentrionalis* they are widely separated from each other, as may be seen in **60**: 1. This peculiarity adds another distinction justifying the separation of the two species. The body of the nephridium has a rich brownish-yellow color (**39**: 9), and is marked by varicose ridges; the surface, more highly magnified, shows very irregular markings, transverse to the long diameter of the tube (**56**: 2*b*, 2*c*). The nephridial tubes viewed in front through the coelomic wall (**60**: 1, 2), run nearly parallel and turning abruptly, pierce the wall and project beyond in the form of prominent nipples (**56**: 7). Dall ('71) describes the external openings of the nephridia in *Dallina floridana* as teat-shaped with very small orifices. Doubtless in related forms this protuberant end will be found, though in *Terebratalia coreanica*, as we shall see, it is in the form of a simple slit in the parietes. The appearance of the orifice in the nephridium of *T. septentrionalis*, viewed directly in front, is shown in **56**: 6. The nipple is nearly circular, the larger diameter being vertical; the opening is circular and an indication of a lozenge-shaped escutcheon is seen surrounding the orifice, this appearance arising from muscle fibers which possibly control the orifice. The interior of the opening, as well as the channel within, is strongly ciliated. It will be seen in **56**: 1, 2, that a band, or bands, quite separate from the ilio-parietal band, originate at the edge of the nephrostome and run ventrally; upon this is found the accessory vesicle as well as clusters of ova. This is the genital band and is well shown in **56**: 1. In **60**: 1, the attitude of the nephridia in relation to the mouth and brachia is shown. In **56**: 4, 5, the appearance of the nephridia in very young specimens is given. The flaring edge of the nephrostome instead of being lamellated has a distinct, thickened rim; the rim of the nephrostome seems to be interrupted, as if its attachment were like that seen in *L. lepidula*, that is, that the band, or wall to which it is attached, forms part of the boundary of the nephrostome. In *T. coreanica*, viewed from the dorsal surface (**55**: 8), the nephrostomes open obliquely backward. The inner surface is marked by thin, sharp, radiating folds which in appearance suggest the actinoid coral, Fungia (**55**: 9). The folds are vertically marked or plicated. A slight constriction is seen just below the nephrostome; it then widens into a thick body and continuing for half the entire length of the nephridium turns abruptly upon itself, tapers slightly, and pierces the anterior wall obliquely, ending in a wide, simple opening more nearly resembling the exterior openings in *L. lepidula* or Discinisca, and in no way resembling Terebratulina (**55**: 8). At **55**: 7, is another drawing showing the attitude of the nephridia in relation to the body. In *Dallina grayii*, the nephrostomes are united by a band and are so close together as to be almost in contact (**56**: 8). The plane of the nephrostome is only slightly inclined to the longitudinal axis of the nephridium, which is straight and tapers only slightly to the exterior opening, which is very wide and simple. A deep constriction is seen on the outer side of the nephridium. The rim of the nephrostome is thrown into deep crenulations (**56**: 9). The nephridium is rose color with deeper longitudinal markings (**39**: 8). The nephridia of *H. psittacea* are quite unlike those of other genera here described, the nephrostomes alone excepted, which bear some resemblance to those of Glottidia. Instead of a long, tapering body with narrow external opening, it is only twice as long as broad and there is only the slightest tapering to the external opening. In the other forms here studied, with the exception of the *Lingulidae*, the diameter of the nephrostome far exceeds that of the body. In Hemithyris, in one example, the diameter of the nephrostome is the same as that of the body, in another it is narrower than the body (**55**: 10, 11). As Hemithyris has two pairs of nephridia, my two sketches probably represent one of each pair, a point I did not make clear at the time of observation. The axis of the nephrostome is at a slight angle to that of the body, is slightly flaring, and the rim is thrown into deep folds which extend within and are strongly ciliated. A sharp constriction marks the junction of the nephrostome with the body of the nephridium which is short and broad. The surface is marked by a few deep, irregular and anastomosing folds; these folds mark the boundaries of the lacunae in which an active circulation is seen; **55**: 10*a* shows a much enlarged view of the edge of the nephrostome and **55**: 11*a* one of the anastomosing folds of the nephridium, greatly enlarged. The marked difference in the form of the external mouths will be noticed; the "heart of Hancock," as well as certain masses which are probably ova, may be seen attached to the genital band.

GENITAL PRODUCTS.

In Glottidia, the masses of eggs fill the perivisceral cavity in compact clusters. A transverse section through the intestine shows a ventral mesentery as thick as the walls of the intestine, an inner vascular space is defined, branches are given off to the right and left, and these send out other bands from which the gonads spring. In these masses to be developed into ova, every stage is seen from the small cell to the distinctly nucleated egg

(**57**: 5, 5*a*). The egg has a radially striated cell membrane, not the *zona radiata* of embryologists (**57**: 5*b*). I have observed at the same period, individuals with the body cavity filled with yellow masses, easily distinguished by the unaided eye as ova, while other individuals were equally filled with white sperm masses. The spermaries form large irregular bunches springing from the genital band; they consist of agglomerations of sperm cells and the spermatozoa are detached in groups (**57**: 2, 2*a*). The irregular shape of the stomachal glands, as well as of the ovarian masses is well shown in **57**: 1, while **57**: 1*a* and 1*b* show the appearance of the two masses respectively. In *L. lepidula*, the ova are in rounded clusters, a clear interspace showing at the end of each egg (**57**: 4). In *L. anatina* the masses recognized as testes were lobulated, these lobules numbering seven or more in a group (**57**: 3). The whole mass was white in color, differing in this respect from the ova. Each lobule was filled with minute, round cells. In another drawing of *L. anatina* (**47**: 7) there appeared an irregular digitated band running midway between the intestine and the oblique muscles on each side which, at the time of observation, I noted as testes. Certain lobular masses in this figure are either immature ova or testes, and if ova, what are the digitated bands? They cannot be testes as the sexes are distinct in Glottidia and presumably in all the *Lingulidae* if not in all the Ecardines. In *D. lamellosa* the eggs are attached in clusters to the gastro-parietal band. In **57**: 7, the attachment of this band is shown running from the sides of the intestine to the outer and posterior dorsal edge of the great occlusor. In the figure, this band is turned forward to show more clearly its relation to the surrounding parts. In **57**: 8 is represented a portion of this band more highly magnified; the strands running off from the edge of the band and loaded with eggs are the result of proliferation; **57**: 9 presents the appearance of four clusters of eggs united by genital strands, and **57**: 10 shows the appearance of a single cluster. The eggs are globular and of all sizes. In the figure may be seen a thread running down on one of the strands, upon which are exceedingly minute cells which are probably immature eggs. The eggs are brownish in color and this is probably their natural color unaffected by their preservation in alcohol. In *Discinisca stella* the eggs are light brown (**57**: 6). Adult individuals were filled to repletion with eggs, and in separating the animal from the rock, eggs escaped in profusion. In *T. septentrionalis*, the eggs are spermaceti-white in color, opaque, and resemble a fine white powder when deposited.

The eggs are thrown out of the pallial cavity and accumulate in piles in front of the animal as well as hang in festoons from the setae. In some instances the eggs were active on the day of their discharge and moved away by the action of the cilia that encircle them; in other instances the eggs did not move away for three days. At **58**: 1 is represented an adult individual in the act of ovipositing. Eggs were found in abundance in individuals measuring only 5 mm. in length and were found in equal abundance in all sizes up to the mature form. These eggs were apparently ripe and ready to be discharged: the dates upon which the animals were found with eggs in this condition were May 31, June 26, July 12, and August 29. An examination of hundreds of adult individuals revealed the fact that in some, the sinuses were entirely free from eggs, while in others they were packed to repletion. In many, what appeared to be *corpora lutea* were observed. The appearance of the eggs in the lacunae is shown in **58**: 2, 3, 4, 6. As previously described, the eggs have been distinctly and repeatedly traced from their dehiscence and escape from the pallial lacunae into the coelomic cavity, their entrance into the nephrostome, their passage, one by one, through the nephridium to their final discharge from the nipple-like exterior openings into the pallial chamber (**58**: 4). Eggs are also found attached to the genital bands and hanging free in the coelomic cavity (**56**: 1, 3). The eggs are of all sizes as shown in **58**: 5, in which a cluster of eggs is represented attached to the genital band. In *T. coreanica* (**57**: 11), the pallial sinuses and lacunae when filled with eggs, are deep purple in color (**39**: 14). The eggs are found in clusters composed of leaf-like processes in radial arrangement (**57**: 13). The clusters were irregularly oval in shape and varied in size (**57**: 12). In **57**: 15, is shown the appearance of one of the radial segments, each leaf holding one or two rows of eggs, with four or five eggs in a row. These leaves were slightly folded in their long diameters, the distal edges rounded like a carpenter's gouge. With transmitted light, the leaves were light purple in color, their outer edges tipped with light yellowish-brown, while the eggs were light pink in color (**39**: 13). There were from twenty to twenty-four rows of leaves in each cluster. A side view of one of these masses presents an imbricated appearance as shown in **57**: 14. Claparède ('69) figures a group of ovaries in a chaetopod annelid, *Pachydrilus verrulosus*, which suggests a similar feature in the egg clusters. The arrangement of the egg clusters in *T. coreanica* is so far unique among the Brachiopoda.

TESTES.

The long disputed question as to whether the sexes are separate or united in the individual is still a debatable one. That the male and female sexual products arise from the same parts is unquestionable, that they do not arise at the same time in one individual, at least in Terebratulina, is, according to my observations, equally certain. I am strongly inclined to believe that in the Testicardines, as well as in the Ecardines, the sexes are separate, yet in Terebratulina I cannot positively aver that an individual filled with clusters of spermatozoa, may not at another time be found with eggs. I have not been able to detect any differences, external or internal, which would suggest sexual variation.

Schulgin found only females in Cistella; Kowalevski, however, states that he found a number of males, but Schulgin asserts that the organs found by Kowalevski preclude all possibility of hermaphroditism. In *T. septentrionalis*, the spermaries are found in the lacunae of the pallium, every portion being filled with this substance (**58**: 11). When the spermaries arise from the genital bands upon which is found the accessory "heart of Hancock," they appear in the form of a cluster of long threads converging to a common centre of attachment, either upon the accessory heart or in its very immediate vicinity. These threads to the number of hundreds form a rounded tuft-like mass twice the diameter of the nephridium at its junction with the nephrostome. The relation of this spermary tuft to the nephridium is shown at **58**: 7. These threads have a knob-like glandular tip colored a deep reddish-yellow (**39**: 10, also **58**: 9, 10). Just below this glandular tip is a fusiform mass of cells which tapers gradually and occupies one fourth the length of the thread; these cells are masses of spermatozoa attached by their heads. The threads are a proliferation from the genital band identical with what was seen in *D. lamellosa.* The spaces between these threads are filled with a granular protoplasmic mass (**58**: 8). In some instances the spermary masses are not cylindrically fusiform. This appearance is due to the separation of clusters of spermatozoa from the mass. The spermary threads enlarge at their ends and are sometimes bent. No eggs were found in specimens bearing these spermary tufts. In specimens in which the pallial lacunae were filled with eggs. the genital bands were also found supporting clusters of eggs; so in individuals in which the spermary tufts were present, the pallial lacunae were also packed with spermatozoa, the little reddish-yellow cells being interspersed in the mass (**58**: 11). The clusters of spermary threads I have found only in Terebratulina. Where should we look for a similar structure in other groups of the animal kingdom? Lang ('96) describes the genitalia of worms as cellular thickenings, sometimes massive knobs, or tufts of strands. Gegenbaur, in his "Elements," in describing the form elements of the sperm in echinoderms, says that they are very generally filamentous structures provided with a small head. The testes of Lumbricus, according to Bloomfield ('80) arise in pairs on each side of a median line, and these start from a membrane much as they do in the Testicardines. There are two pairs and each cell of the testis itself is the source of many spermatozoa. He applies the name spermatospore to the constituent cell of the testis. The spermatoblasts, as a rule, stand out like buds from the cells which generate them. "When the spermatoblasts have reached a suitable size the coat of protoplasm, which has been enveloping the nucleus, begins in each case to collect a small cup or knob-like mass at the distal end." This description, as I shall presently show is certainly like the granular appearance seen on the accessory vesicles of Terebratulina during genital activity. It may be observed that these bodies described by

Bloomfield in Lumbricus arise in close proximity to the nephrostomes. Beddard ('89) also shows that in *Acanthodrilus annectens*, the testes are in close proximity to the inner mouths of the nephridia. From these descriptions I am led to believe that it is among the chaetopod worms we are to look for structures similar to what has just been described in Terebratulina.

ACCESSORY HEARTS.

These curious organs have already been fully described by authors and have been briefly alluded to here in connection with associated parts. It is left for me only to describe their appearance in life. We have found that they really occur on separate strands which are not aligned with the ilio-parietal band. I expressed the conviction ('73b) that these organs did not bear Hancock's interpretation, and that they properly belong to the genital system and not, as stated by him, to the circulatory system. Subsequent studies of these parts in Terebratulina and Terebratalia have only strengthened me in this conviction; yet precisely what part they play in this role I am at a loss to say. The form and size of this vesicle vary more or less in every individual, as may be judged by an examination of plate **59**, which is devoted to a representation of its appearance in *T. septentrionalis* and *T. coreanica.* Whether the animal be charged with ova or spermatozoa, the vesicle is always present. Sometimes there are two or more of these vesicles in close proximity, and this duplicature has been noted by Hancock. It would seem that if this organ functioned as a heart, there ought to be some constancy about it in form and size. In some individuals the vesicle has a long peduncular attachment and is testicular in shape (**59**: 4, 7). In a careful study of a number of these vesicles, there was found no cavity within, and in no case was there seen any vascular connection with the genital band from which it sprang. The mass appeared to be glandular throughout and was distinctly tinged with a reddish-yellow, like the nephridium. In a number, the surface was covered with globular, transparent cells tipped with minute yellow granules apparently identical with the knobs already described as tipping the filiform spermaries which. we saw, arose from the vesicle, or from its immediate vicinity and also identical with the reddish-yellow cells marking the spermaries in the pallial lacunae. In some, a secondary vesicle was found (**59**: 3*a*), and in others incipient vesicles were budding in close proximity (**59**: 1). A number of my drawings show externally a granular surface and a structure within, that in one case seemed to be a round, distinct cavity with light reddish-yellow walls. In another instance, I observed what appeared to be an elongated cavity which made nearly a complete turn within the vesicle, one extremity being larger than the other (**59**: 2). In another case a varicose mass ran over the surface of the vesicle (**59**: 4, 7). Under various pressures, no fluid, or other contents could be forced out at its point of attachment with the genital band, nor was any opening or duct found upon its surface. There was a slight glandular thickening on the edge of the genital band (**59**: 8), and a similar thickening was found on the posterior edge of the ilio-parietal band, as shown in **56**: 2. In *T. coreanica*, the edge of the ilio-parietal band is not only thickened, but it has the reddish-yellow coloration that we have seen associated with the spermaries, and which also tinges the vesicle in those forms studied. This colored glandular thickening of the edge apparently runs from the central vesicle to the accessory vesicle without a break. In **39**: 12, this feature is shown in color. The central vesicle resting on the posterior dorsal surface of the stomach was bluntly triangular in shape, with the base anterior, and the sides of the triangle strongly lobulated. From the median line in front, the band, which Hancock mistook for an artery, divides and passes forward and downward on the sides of the stomach and then, laterally, making three short flexures, turns abruptly backward to terminate in the accessory vesicles. It may be observed that these flexures are the result of the loose folding of the ilio-parietal band and this so-called artery arises from the edge of it. It will be observed that this structure, from the central to the lateral vesicles, is distinctly tinged a reddish-yellow and, as before observed, it is the color which tips the filiform spermaries and other parts of the genital apparatus already described, but I have not observed this color associated with the eggs in Terebratulina, though the purple ovarian leaflets in *T. coreanica* were tipped with it. It is a very significant fact that no blood vessel, sinus, or lacune shows a trace of this color. In another specimen of *T. coreanica*, the central vesicle was oblong and was thrown into a series of folds or plications (**59**: 10, 11). The folds were slightly darker in color. With transmitted light, no cavity was detected within, and it seemed to be made up of irregular masses of radiating tissue which appeared glandular. No channel could be detected at its point of attachment, nor was a trace of muscle fibers discerned. The lateral or accessory vesicles (**59**: 12, 13), seem to have the same structure without folds or plications. The exterior surface of the accessory vesicles was granulated with minute cells, with a yellowish substance interspersed.

Precisely what role these various parts play in the organization of the animal, I have not made out, but that they are intimately related to the genitalia, there can be no doubt. It may be added here that while the nephridia, as well as many other parts of the anatomy, in all species examined, reveal the presence of ramifying lacunae through which the blood is seen rapidly circulating, these vesicles, central and accessory, are about the only organs which show no trace of any circulating fluid within or without.

EXTERNAL GLANDS.

A curious paired organ of which I published a short account some years ago ('72) has, with this exception, never been observed before. These organs are found clustered around the exterior nipple-like openings of the nephridia in *T. septentrionalis*. Plate **60** is devoted to illustrations of these bodies. They form conspicuous, white, lobulated masses arising from the space between the external orifices of the nephridia. The lobules, to the number of ten or twelve, vary in shape from one another, and are by no means alike on each side; in this respect forming a marked exception to the strictly bilateral and symmetrical repetition of parts in the Brachiopoda. In one instance a peculiar lobulated structure ensheathed the nephridial tube, apparently within the coelomic wall (**60**: 8). It seemed to be of the same nature as the external glands. A distinct wall surrounds each lobule, though this wall varies in thickness, being somewhat thicker at the extremities. The lobules stand quite free from each other and have a narrow base of attachment. They all seemed to be clothed with a ciliated epithelium. Under pressure, irregular granules were forced out and these vibrated in such a manner that I first mistook them for spermatic particles. At **60**: 12, is represented the appearance of these lobulated masses as seen from below. They stand quite free and prominent from the coelomic wall. Between these masses is seen a distinct prominence; viewed from in front, this prominence is bordered by an encircling line (**60**: 6). In **60**: 1, its position in relation to the mouth and other parts is shown; in this figure, also, a clear idea may be had of the position of the external glands in relation to other parts of the structure. In **60**: 13, a rough outline is given representing a longitudinal section of *T. septentrionalis* for the purpose of indicating the exact position of the external glands in relation to other parts of the anatomy. The spiculae which abound in the pallium, brachia, and cirri of this animal, are also found in the external layer of these glands (**60**: 5, 7, 10).

Precisely what may be the function of these external glands I do not know. Mucous secretions occur abundantly about the external openings of the nephridia and the mouth, and it may be that these are simply mucous glands. Whether they may be compared to the dermal glands of the chaetopod worms is a question, though it is stated that the dermal glands in worms form an investment for the ova; but the ova of Terebratulina are not invested with mucus. With the idea that they are glandular, I have given to them the name of external glands. I have not observed them in other Testicardine forms, though they will doubtless be found. From their intimate association with the external ducts of the nephridia, it seems reasonable to believe that in some way they are connected functionally with the genitalia.

The nearest approach to these organs has been described by Schulgin in Cistella. He says, "Argiope [= Cistella] has not far from the mouth, on the integument an accumulation of cells which play the part of an organ of sense. This organ consists of two longish heaps of cells lying parallel to one another, of which that lying nearer the mouth is formed of specific cells and that farther away from it of epithelial cells." Schulgin figures these organs as projecting from the coelomic wall and describes them as one above another in a median line. He makes no remark about their relation to the external openings of the nephridia, yet there would seem to be some relation between these bodies he describes and the external glands.

EARLY STAGES.

In the previous pages, reference has often been made to the early stages of the shell and the soft parts of these animals; there are other features to be briefly alluded to, however, and in plate **61** I have brought together a number of outlines of the early and nepionic stages of various forms for purposes of comparison. The illumination which Beecher ('92) has shed upon the phylogeny of the Brachiopoda from what little we yet know of the ontogeny, has been based upon material of this kind. In this study he has found a confirmation of certain principles of evolution first enunciated by the lamented Hyatt. In the plate above referred to, I have taken the liberty of reproducing for convenience of comparison four outlines of the early stages of Terebratulina from my Embryology of that species. In **61**: 1 is represented the posterior portion of the shell of an undescribed Lingula from Nagasaki. I made only the briefest observation of the animal, and have no idea of the meaning of the structure outlined within. The nepionic outline with the straight posterior margin is similar to that seen in *L. lepidula* (**42**: 3, 4), except that it is somewhat broader. In *D. lamellosa*, at an early stage, the bases of the oblique muscles are slightly flaring, a feature not seen in maturity. In a very early stage (**61**: 11), these muscles are excessively flaring at their point of attachment. In a stage where the brachia are well formed, numbering thirty or more cirri, the various muscles may be clearly defined, except that the separation of the anterior occlusor into two muscles is not apparent though the lateralis is well developed. The anterior and posterior occlusors are compacted within a short space. In **60**: 10, a supernumerary muscle, apparently a repetition of the obliquus posterior, is shown on the right side. Blochmann has figured, in an adult specimen, the same anomaly on the left side. The disproportionate size of the anterior and posterior setae in the young is well shown in the drawings. The nepionic shell (**61**: 11) is absolutely circular; in this figure the few cirri, seven or eight in number, are turned towards the mouth. The coelomic wall shows distinctly two sets of muscles crossing each other obliquely (**61**: 8*a*). A septum seems to divide the two sides anteriorly. The setigerous follicles start from the edge of the coelomic wall and as the animal grows, this line is carried beyond the coelomic wall. The same displacement is seen in other parts: as the animal increases in diameter the attachments of the various muscles, which were compacted before, become more widely separated. The sinuses and lacunae are wide and irregularly branching, the main branches showing the ciliary ridges. The stomachal glands, in an early stage, appear as solid masses (**61**: 10), but shortly after, break up into numerous coeca. In all the early stages of *D. lamellosa*, the stomach is distinctly bulbous. In the young of *D. stella*, the anterior setae are much longer than in the corresponding stage of *D. lamellosa* (**61**: 3). In quite an advanced stage, the stomach is large, round, and apparently fills the entire coelomic cavity (**61**: 2).

In the young of *H. psittacea* (**61**: 17), the shell is quadrate, slightly narrowing behind, with corners widely rounded. The peduncular portion is large and more than one third the length of the dorsal shell. The peduncular opening is very large. In this stage, the lophophore appears circular, as in the early stages of Terebratulina; the stomachal glands show two or three coeca on each side, the setae are long and extremely tenuous, and appear only on the anterior and lateral portions of the pallium; in the specimen figured, seventeen were counted. Near the peduncle, the muscles and interlocking processes of the shell were partially made out.

Since these pages were written, a very interesting communication has appeared, on the habits of Lingula by Naohide Yatsu.[1] His notes relate to the large Lingula, *L. anatina*. He remarks on the great vitality of the species in surviving conditions which kill most other marine animals. He records that his friend, Mr. Namiye, detected the burrows of this Lingula by the appearance of three holes on the surface of the mud in which they were imbedded. It would appear from this observation that the species formed the three setal tubes as described in *L. lepidula* (p. 319). He also presents evidence showing that *L. anatina* lives more than one year. His memoir on the development of Lingula is announced as in press, to be published in the journal of the college of science of the imperial university, Tokyo.

Professor Edwin G. Conklin has kindly sent me the advanced proofs of a forthcoming memoir of his on the embryology of a brachiopod (*Terebratulina septentrionalis*), which will soon be published by the American philosophical society in vol. 41, no. 168. In this communication he shows that the embryo of this brachiopod, at least, belongs to the trochophore type and bears a close resemblance to Phoronis and a certain resemblance to the Polyzoa. He expresses the opinion that the Brachiopoda, Polyzoa, and Phoronis should be classed together in a phylum distinct from the Annelida, Mollusca, or Chaetognatha.

---

[1] Annotationes zoologicae Japonenses, March, 1902.

With the appearance of this contribution and the promised one by Yatsu on the development of Lingula, a great flood of light will be thrown upon the relations of this ancient group.

Professor Conklin in his memoir refers to the work of Mr. Ikeda[1] and says, "Mr. Ikeda has given by all odds the most complete account of the embryology of Phoronis yet published." In view of the remarkable work being done by Japanese scholars in embryology, histology, and morphology as shown in the various memoirs by Mitsukuri, Iijima, Watase, Ishikawa, Sasaki, Oka, Miyoshi, Gotō, Inaba, Hatta, Tanaka, Kishinouye, Matsuda, Hiroto, Hirase, Ikeda, and others we may safely say that in the future the greatest illumination on this ancient and closed type of animals will come from the investigations of the young naturalists of Japan. Their work is abreast of the best work done abroad. Their observations are keen, their artistic skill is accurate and refined, their lithographers we would gladly utilize for the reproduction of our own drawings. Japan is the home of the brachiopods. While European and American naturalists have but few forms to study, not only have the Japanese about all the material we have, but their seas contain many genera which we do not find. We may, therefore, safely look to them for further elucidation of this fascinating group of animals.

LITERATURE.

Barrett, L.

'55. Notes on the Brachiopoda observed.... on the coast of Norway. Annals and mag. of nat. hist., 2d series, vol. 16, p. 257–259, 4 figs.

Beddard, Frank E.

'89. On the structure of three new species of earthworms, etc. Quart. journ. micros. sci., new series, vol. 29, p. 101–131, pl. 12–13.

Beecher, C. E.

'91. Development of the Brachiopoda. Part 1. Introduction. Amer. journ. sci., 3d series, vol. 41, p. 343–357.

'92. Development of the Brachiopoda. Part 2. Classification of the stages of growth and decline. Amer. journ. sci., 3d series, vol. 44, p. 133–155, 1 pl., fig. 1–36.

van Bemmelen, J. F.

'83. Untersuchungen über den anatomischen und histologischen bau der Brachiopoda Testicardinia. Jenaische zeitschr. f. naturwissensch., bd. 16, p. 88–161, pl. 5–9.

---

[1] Iwaji Ikeda; Observations on the development, structure, and metamorphosis of Actinotrocha. Journal of the college of science, imperial university, Tokyo, vol. 13, part 4, p. 507–592, 6 plates.

Beyer, H. G

’86. Study of the structure of *Lingula* (*Glottidia*) *pyramidata* Stim. (Dall). Studies from the biological laboratory, Johns Hopkins university, vol. 3, p. 227–265, pl. 14–17.

Blochmann, Friedrich.

’01. Untersuchungen uber den bau der brachiopoden. Jena: verlag. v. Fischer.

Bloomfield, J. E.

’80. On the development of the spermatozoa. Part 1. Lumbricus. Quart. journ. micros. sci., new series, vol. 20, p. 79–89, pl. 6, 1 fig.

Brooks, W. K.

’79. The development of Lingula and the systematic position of the Brachiopoda. Chesapeake zoological laboratory, Johns Hopkins university, p. 35–112, pl. 1–6.

Carpenter, W. B.

’56. On the minute structure of certain brachiopod shells; and on vegetable cell-formation. Annals and mag. of nat. hist., 2d series, vol. 17, p. 502–506.

Claparède, E.

’69. Les annélides chétopodes du golfe de Naples. Part 2. Mém. soc. de phys. et d’hist. nat. de Genève, t. 20, 1ère part., p. 1–225, pl. 17–31.

Crane, Agnes.

’92. Recent observations on the anatomy and development of the Brachiopoda. Natural science, (London), vol. 1, no. 8, p. 603–611, 1 fig.

’93. New classifications of the Brachiopoda. The geol. mag., (London), new series, vol. 10, p. 318–323.

Dall, W. H.

’71. Report on the Brachiopoda, etc., with a revision of the *Craniidae* and *Discinidae*. Bull. mus. comp. zoöl., vol. 3, no. 1, p. 1–45, pl. 1–2.

Davidson, Thomas.

’86–’88. A monograph of recent Brachiopoda. Trans. Linn. soc. London, 2d series, vol. 4, p. 1–248, pl. 1–30, fig. 1–24.

Ekman, T.

’96. Beiträge zur kenntnis des stieles der brachiopoden. Zeitschr. f. wissensch. zoöl., vol. 62, p. 169–249, pl. 6–9, fig. 1–6.

François, Ph.

’91. Choses de nouméa. 2. Observations biologiques sur les lingules. Archiv. de zoöl. expériment., 2ième série, t. 9, p. 231–239, 2 figs.

Gegenbaur, Carl.

’78. Elements of comparative anatomy. English ed., 8°, ill.

Gill, T.

’73. On the primary divisions of the brachiopods. Annals and mag. of nat. hist., 4th series, vol. 12, p. 201–203.

Hancock, A.

’59. On the organization of the Brachiopoda. Philosoph. trans. royal soc. London, vol. 148, p. 791–869, 15 pls.

Huxley, T. H.

’56. Contributions to the anatomy of the Brachiopoda. Proc. royal soc. London, vol. 7, p. 106–117, fig. 1–2.

Joubin, L.

’86. Recherches sur l’anatomie des brachiopodes inarticulés. Archiv. de zoöl. expériment., 2ième série, t. 4, p. 161–303, pl. 7–15, fig. 1–3.

’92. Recherches sur l’anatomie de *Waldheimia venosa* (Sol.). Mém. soc. zoöl. de France, t. 5, p. 554–583, fig. 1–26.

King, W.

’70. On the histology of the test of the class Palliobranchiata. Trans. royal Irish acad., vol. 24 (science), p. 439–455, pl. 26.

Kowalevski, A. A.

’74. Observations on the development of Brachiopoda. (In Russian.) Proc. imper. soc. amat. naturalists, Moscow.

Lang, Arnold.

'96. Textbook of comparative anatomy. Part 2. London. Transl. by H. M. and M. Bernard.

Lankester, E. R.

'73. Summary of zoölogical observations made at Naples in the winter of 1871–'72. Annals and mag. of nat. hist., 4th series, vol. 11, p. 81–97, fig. 1–3.

Macdonald, J. D.

'61. On the physiology of the pallial sinuses of the Brachiopoda. Trans. Linn. soc. London, vol. 23, part 2, p. 373–375, pl. 35.

Morse, E. S.

'70. The Brachiopoda, a division of Annelida. Amer. journ. sci. and arts, 2d series, vol. 50, p. 100–104, fig. 1–3.

'71. On the early stages of *Terebratulina septentrionalis* (Couthouy). Mem. Boston soc. nat. hist., vol. 2, p. 29–39, pl. 1–2.

'72. On the oviducts and embryology of Terebratulina. Amer. journ. sci. and arts, 3d series, vol. 4, p. 262–263, pl. 3.

'73a. Embryology of Terebratulina. Mem. Boston soc. nat. hist., vol. 2, p. 249–264, pl. 8–9.

'73b. The systematic position of the Brachiopoda. Proc. Boston soc. nat. hist., vol. 15, p. 315–372, pl. 1, fig. 1–42, 1–6.

'78. On Japanese Lingula and shell mounds. Amer. journ. sci. and arts, 3d series, vol. 15, p. 156–157.

Owen, R.

'35. On the anatomy of the Brachiopoda of Cuvier, etc. Trans. zoöl. soc. London, vol. 1, p. 145–164, pl. 22–23.

Schuchert, C.

'93. A classification of the Brachiopoda. Amer. geologist, vol. 11, p. 141–167, pl. 5.

'97. A synopsis of American fossil Brachiopoda including bibliography and synonymy. Bull. U. S. geol. survey, no 87, 464 pp., 1 pl., fig. 1–6.

Schulgin, M. A.

'84. *Argiope kowalevskii.* (Ein beitrag zur kenntniss der brachiopoden.) Zeitschr. f. wissensch. zoöl., bd. 41, h. 1, p. 116–141, pl. 8–9.

Semper, Carl.

'62, '64. Ueber Lingula. Zeitschr. f. wissensch. zoöl., bd. 11, p. 100–104 ; bd. 14, p. 424.

Shipley, A. E.

'83. On the structure and development of Argiope. Mittheil. zoöl. sta. Neapel, bd. 4, p. 492–520, pl. 39–40.

Sollas, J. W.

'86–'87. The "coecal processes" of the shells of brachiopods interpreted as sense organs. Scientific proc. royal Dublin soc., new series, vol. 5, p. 318–320, 1 fig.

Vogt, Carl.

'45. Anatomie der *Lingula anatina.* Nouv. mém. soc. Helvét. sci. nat., t. 7, 2 pls.

Williams, T.

'51. Report on the British Annelida. Report British ass'n for the advancement of science, p. 159–272.

EXPLANATION OF PLATES.

ABBREVIATIONS USED.

a. — anus.
a. b. l. — anterior branch of lateral sinus.
a. cl. — anterior cluster of setae.
a. f. — anterior folds of pallium.
a. h. — accessory "hearts of Hancock."
ap. — aponeurosis of muscle of main pallial sinus opening.
a. p. s. — anterior pallial sinus.
az. — azygos process.
b. — brachia.
b. f. — brachial fold.
b. g. — brachial groove.
b. g. m. — brachial groove muscles.
b. l. — border lip of pallium.
b. p. — border of pallium.
b. s. — brachial sinus.
c. — collar.

c. c. — coelomic cavity.
ci. — cirrus or cirri.
ci. m. — cirri muscles.
c. l. — corpora lutea.
c. m. — cutaneous muscles.
c. o. — central oblique muscle.
c. r. — ciliary ridge.
cru. — crura.
c. s. — coelomic sinus.
c. t. — connective tissue.
c. w. — coelomic wall.
D. — dorsal shell.
di. — divaricator muscle.
e. — eggs.
e. e. — ectodermal epithelium.
e. g. — external glands.
en. — endothelial lining of pallium.
e. o. — external oblique muscle.
e. s. — encircling sinus.
f. — faeces.
f. f. — folds of funnel.
f. y. — fibrous yoke.
g. — gut.
g. a. — gill ampullae.
g. b. — genital band.
g. b. s. — great brachial sinus.
g. en. — glandular enlargements.
g. f. — gill fold.
g. g. — glandular growth on edge of ilio-parietal band.
gl. — gland cells.
gp. — gastro-parietal band.
g. p. a. — ganglion of posterior adductor muscles.
gp. m. — gastro-parietal muscle.
g. t. — glandular tip of spermary thread.
H. — "heart of Hancock."
i. — intestine.
i. b. — inner band of pallial muscles.
in. — infra-oesophageal ganglion.
ip. — ilio-parietal band.
i. t. — inner tube.
l. — lateralis muscle.
la. — lacunae.
l. b. — lateral branch of anterior sinus.
l. i. — lumen of intestine.
l. p. — lateral parietal band.
l. p. s. — lateral pallial sinus.
l. s. — lateral septa.
m. — mouth.
m. cl. — median cluster of setae.
m. f. — muscle fiber.
m. g. — median groove of pallium.
m. p. — main pallial sinus.
m. s. — median septum.
m. si. — median sinus.
m. t. — muscular tube.
n. — nerve.
n. b. — nephridium body.
n. ba. — nephridial band.
ne. — nephridium.
nf. — nephrostome.
n. o. — nephridial opening (external).
n. p. — nephridial papillae.
n. s. — natural size.
n. t. — nephridial tube.
o. a. — obliquus anterior muscle.
o. b. — outer band of pallial muscles.
oc. — anterior occlusor muscle.
oc. I. — occlusor externus muscle.
oc. II. — occlusor internus muscle.
oe. — oesophagus.
o. e. — obliquus externus muscle.
o. h. s. — outer horny sheath.
o. i. — obliquus internus muscle.
o. l. s. — opening of lateral sinus.
o. m. — obliquus medius muscle.
o. p. — obliquus posterior muscle.
o. p. s. — outer pallial sinus.
o. s. — opening of main pallial sinus.
ot. — otocyst.
ov. — ovaries.
pa. — parasite.
p. b. — posterior band.
p. b. l. — posterior branch of lateral sinus.
p. c. — peduncular cavity.
p. ca. — peduncular canal.
p. ch. — pallial chamber.
p. cl. — posterior cluster of setae.
pe. — peduncle.
ph. — pharynx.
ph. g. — pharyngeal gland.
ph. m. — pharyngeal muscles.
p. m. — perivisceral membrane.
p. n. — peduncle notch.
p. o. — posterior occlusor muscle.
pro. — protegulum.
p. s. — peduncular septum.
p. si. — peduncular sinus.
r. — rectum.
r. b. — retractor brachia muscle.
re. — rectus muscle.
ro. — rostrum.
s. — sinus at base of cirri.
s. b. — shell border.
s. b. s. — small brachial sinus.
se. — setae.
s. f. — setigerous follicles.
s. g. — stomachal glands.
s. g. d. — stomachal gland duct.
s. g. o. — stomachal gland opening.
s. m. — setal muscles.
sp. — spermatospore.
spe. — spermaries.
spi. — spiculae.
spm. — spermatozoa.
sp. t. — spermatic threads.
s. s. — supporting substance.

s. t. — setal tubes.
sto. stomach.
su. — supernumerary muscle.
t. — testes.
V. ventral shell.
v. m. — ventral mesentery.
v. r. — ciliary ridge of visceral sinus.
v. t. vascular twig.

PLATE 39.

Reproductions of original drawings to illustrate color in living Brachiopoda.[1]

Fig. 1. *Lingula lepidula* from ventral side.
Fig. 2. Brachia of *L. lepidula* showing color of border and cirri.
Fig. 3. Anterior portion of pallium of *L. lepidula.*
Fig. 4. Portion of pallium of *Glottidia pyramidata* showing three rows of gill ampullae and pigmentation between.
Fig. 5. View of pallium showing anterior pallial folds.
Fig. 6. Enlarged view showing pigmentation of pallial fold.
Fig. 7. Cirrus of *G. pyramidata* showing pigmentation.
Fig. 8. Nephridia of *Dallina graysii.*
Fig. 9. Nephridia of *Terebratulina septentrionalis.*
Fig. 10. Spermary thread of *T. septentrionalis.*
Fig. 11. Border of pallium of *Terebratalia coreanica.*
Fig. 12. Stomach and immediate parts of *T. coreanica.*
Fig. 13. Ovarian leaflets of *T. coreanica.*
Fig. 14. Pallium and pallial sinuses of *T. coreanica* filled with eggs.

PLATE 40.

Appearance in life of various forms.

Fig. 1 to 5. *Glottidia pyramidata.*

Fig. 1. Dorsal view, at rest.
Fig. 2. Dorsal shell, oscillating.
Fig. 3. Side view, dorsal shell elevated.
Fig. 4. Side view, dorsal shell depressed.
Fig. 5. Peduncle showing vermiform convolutions with posterior end inclosed in sand tube.

Fig. 6 to 15. *Lingula lepidula.*

Figs. 6, 7, 8, and 9. Various attitudes.
Fig. 10. Burrow in sand.
Fig. 11. Eleven individuals attached to bottom of bowl by sand accretions; compare with Glottidia (**41** : 13).
Figs. 12 and 13. Showing attitude in sand, with setal tubes formed.
Fig. 14. Front view showing anterior pallial folds and setal tube openings.
Fig. 15. Side view with lateral setae vertical and meeting.

Fig. 16 to 18. *Lingula anatina.*

Fig. 16. Showing end of peduncle encased in mud tube.
Fig. 17. Young specimen with brachia extended laterally.
Fig. 18. Dorsal view of partially grown individual.
Fig. 19. Side view of *Discinisca lamellosa* from alcoholic specimen.

---

[1] For explanation of details of these figures see succeeding plates.

PLATE 41.

Life attitudes of *Glottidia pyramidata.*

Fig. 1 to 10. Various attitudes in the sand.

Fig. 3. With peduncle broken away, burying itself head first in the sand.

Fig. 11. Anterior portion projecting above the sand with a pile of sand in front.

Fig. 12. With peduncle broken away, burying itself sidewise.

Fig 13. Eight individuals attached to bottom of bowl by rude sand burrows; compare with similar group of *Lingula lepidula* (**40**: 11).

Fig. 14. With case of sand around posterior end of body.

Figs. 15 and 16. Injured peduncle with inner tube partially withdrawn from outer sheath

Fig. 17 to 25. Various attitudes, some with sand tube preserved.

Fig. 26 to 30. Portions of peduncle broken away, with globular masses of sand at end.

Fig 31 to 33 Various attitudes.

PLATE 42.

Dorsal and ventral shells of various forms.

Figs. 1 and 2. *Glottidia pyramidata*, dorsal and ventral shells.

Fig. 3 to 8. *Lingula lepidula.*

Fig. 3. Ventral view of posterior end showing protegulum and portion of peduncle.

Fig. 4. Posterior end, ventral view. Arrows indicate direction of circulation.

Fig. 5. Outlines of shells in life showing extent of individual variation.

Fig. 6. Appearance of shells when dried.

Figs. 7 and 8. Posterior end of dorsal and ventral shells.

Fig 9 to 13. *Discinisca lamellosa*

Fig. 9. Orbicular nucleus.

Fig. 9*a*. Polygonal structure of shell.

Fig. 9*b*. Fracture of shell margin.

Fig. 10 to 13. Dorsal and ventral shells showing protegulum stage.

Fig. 14 to 17. *Discinisca stella.*

Fig. 14. Portion of ventral shell showing radiating ridges.

Fig. 15. Greatly enlarged view of two ridges.

Fig. 16. Nucleus of ventral shell.

Fig. 17. Longitudinal section. (The lower of the two figures should have been lettered 17*a*.)

Fig. 17*a*. Dorsal view of ventral shell.

PLATE 43.

Peduncles of Lingula, Glottidia, Discinisca, and Terebratulina.

Fig 1 to 3. *Lingula lepidula*, showing severed ends of peduncle.

Fig. 4 to 13. *Glottidia pyramidata.*

Fig. 4. Showing withdrawal of inner tube and muscular tube from end of outer sheath.

Fig. 5. Portion of peduncle.

Figs. 6, 7, and 10. Appearance of peduncle after death and separation from body.

Figs. 8 and 9. Portions of peduncle; arrows indicate direction of circulation.

Figs. 11 and 12. Transverse sections of peduncle.

Fig. 13. Peduncle as it issues from body.

Fig. 14. Peduncular end of *Discinisca lamellosa* from ventral surface, showing peduncular muscles.

Fig. 15. End of peduncle of young of *Terebratulina septentrionalis.*

PLATE 44.

Setae of various forms.

Figs. 1 and 2. Setae of *Glottidia pyramidata.*

Fig. 1. Setae projecting from side of pallium, with color indicated by shading.

Fig. 2. Proximal portion of seta.

Fig. 2*a*. Termination of seta.

Fig. 3 to 5. Setae of *Discinisca stella.*

Fig. 3. Various forms of setae.

Figs. 4 and 5. Appearance of setae springing from pallium.

Fig. 6 to 10. Setae of *Discinisca lamellosa.*

Fig. 6. Setae of extreme young.

Fig. 7. Setae of adult.

Fig. 8. Portion of pallium showing setae springing from setigerous follicles with setellae turned back.

Figs. 9 and 10. Setae of young.

Fig. 11. Seta from extreme young of *T. septentrionalis,* with setigerous follicle.

Fig. 12. Border of pallium of *Terebratalia coreanica* showing setae.

Fig. 13. Border of pallium of *Terebratalia minor* showing setae.

Fig. 14. Seta of *Laqueus rubellus.*

Fig. 15. Border of pallium of *Hemithyris psittacea* showing setae.

PLATE 45.

Various life attitudes of the brachia of *Glottidia pyramidata* and *Lingula lepidula.*

Fig. 1 to 12. *Glottidia pyramidata.*

Fig. 1. Dorsal view.

Fig. 2. Ventral view.

Fig. 3. Dorsal view.

Figs. 4, 5, 6, and 10. Anterior views.

Fig. 7. Oblique anterior view with shells slightly parted.

Fig. 8. View of brachia from ventral side.

Fig. 9. Left brachium, ventral surface uppermost.

Figs. 11 and 12. Lateral view.

Fig. 13 to 15. *Lingula lepidula.*

Fig. 13. Dorsal view.

Fig. 14. Anterior view.

Fig. 15. Ventral view.

PLATE 46.

Brachia and cirri of various forms.

Figs. 1 and 2. End of cirrus of *G. pyramidata.*

Fig. 3. Portion of brachia with collar and one cirrus of *L. lepidula.*

Fig. 4. Brachia of *L. lepidula*, with cirri removed.

Fig. 5. Terminal half of cirrus of *L. lepidula*, showing pigmentation.

Figs. 6 and 6*a*. Cirrus of *L. anatina*.

Fig. 7. Brachia of small Lingula, species unknown, from Nagasaki, Japan.

Fig. 8. Anterior end from ventral side of above species showing notches in ventral shell.

Fig. 9. Cirrus of *D. stella*.

Fig. 10. Transverse section of brachium of *D. lamellosa*, made at point marked A, B, on fig. 2, plate **49**.

Fig. 10*a*. Highly magnified view of gland cells from small brachial sinus.

Fig. 10*b*. Portion of cirrus.

Figs. 11 and 12. Young *T. septentrionalis* showing cirri projecting beyond border of shell.

Fig. 13. Anterior view of *T. coreanica*, showing brachia.

Fig. 14 to 18. *Hemithyris psittacea*

Fig. 14. Brachial coils projecting.

Fig. 15. One brachium greatly extended.

Fig. 16. Brachia slightly uncoiled.

Fig. 17. Portion of brachia with surrounding parts from median line.

Fig. 17*a*. Portion of brachium near mouth showing extreme mobility of collar.

Fig. 18. A few cirri.

Fig. 18*a*. Portion of cirrus highly magnified.

PLATE 47.

Details of structure.

Fig. 1 to 3. *Glottidia pyramidata*.

Fig. 1. Dorsal shell removed exposing coelomic cavity, from which have been taken the stomachal glands and genital products.

Fig. 2. Longitudinal section in median line.

Fig. 3. Transverse section of right half of pallial region showing gill fold, gill ampullae, etc.

Fig. 4 to 6. *Lingula lepidula*.

Fig. 4. Brachia with anterior part of alimentary tract showing pharyngeal glands.

Figs. 5 and 6. Stomach and parts adjoining, showing contracted and extended attitudes.

Fig. 7. Dorsal view of *L. anatina*.

PLATE 48.

Details of structure.

Fig. 1. Musculature of *G. pyramidata*.

Fig. 2. Musculature of *L. lepidula*.

Fig. 3. Posterior portion of body of *G. pyramidata*

Fig. 4. Anatomy of *L. lepidula* from ventral side.

Fig. 5 to 8. Details of anatomy of *L. lepidula*.

PLATE 49.

Details of structure.

Fig. 1 to 6. General anatomy of *Discinisca lamellosa*

Fig. 1. Dorsal shell and most of the genital products removed

Fig. 2. General view showing pallial sinuses, lacunae, etc.

Fig. 3. Longitudinal section.

Fig. 4. Bend of intestine and peduncular canal.

Fig. 5. Peduncular canal.

Fig. 6. Stomach with gastro- and ilio-parietal bands.

Fig. 7. *D. stella*, showing head and brachia.

PLATE 50.

Details of alimentary tract of various forms.

Fig. 1 to 10. *Glottidia pyramidata.*

Figs. 1 and 2. Longitudinal sections of mouth parts.

Figs. 3 and 4. Mouth and brachia from ventral side showing mobility of the lips.

Fig. 5. Dorsal view of pharyngeal region.

Fig. 6. Roof of pharynx from inside, showing triturating ridges.

Figs. 7 and 8. Ventral and dorsal views respectively of stomach and portion of intestine.

Fig. 9. Transverse section of intestine showing attachment of ilio-parietal band.

Fig. 10. Anus.

Figs. 11 and 12. Rectum and anus of *L. lepidula.*

Fig. 13. Portion of right coelomic wall of *D. lamellosa* showing anus.

Figs. 14 and 15. Gut of *D. lamellosa* from an early stage.

Fig. 16. Section of gut of *T. septentrionalis.*

Fig. 17. Digestive tract of *H. psittacea*, with stomachal glands removed.

Fig. 18. Anterior portion of digestive tract of *H. psittacea* showing stomachal glands.

PLATE 51.

Stomachal glands, sense organs and nerves of various forms.

The following figures represent a single coecum, or a cluster of coeca of the stomachal glands, unless otherwise mentioned.

Fig. 1. *G. pyramidata.*

Fig. 2. *L. anatina.*

Figs. 3, 4, and 5. Showing the entire cluster on one or both sides of the stomach of young *D. lamellosa.*

Fig. 6. *D. stella.*

Figs. 7 and 8. *T. septentrionalis.*

Fig. 9. *T. coreanica.*

Figs. 10 and 11. *H. psittacea*, young.

Fig. 12. *H. psittacea*, adult.

Fig. 13. *Dallina grayii.*

Fig. 14. Longitudinal section of mouth parts of *G. pyramidata*, showing infra-oesophageal ganglion and nerve.

Fig. 15. Pallial folds with pigmentation, supposed to be sensitive to light, *idem.*

Fig. 16. Greatly enlarged view of pigmentation of one fold.

Figs. 17 and 18. Nerve and otocyst of *L. lepidula.*

Fig. 19. Nerve with nerve twigs and section of nerve of *G. pyramidata.*

Fig. 20. Otocyst of *L. anatina.*

PLATE 52.

Nerves and other details of various forms.

Figs. 1 and 2. Otocyst and surrounding parts of *L. lepidula.*

Fig. 3. Infra-oesophageal ganglia of *D. stella.*

Fig. 4. Right half of coelomic cavity of *D. lamellosa*, showing oblique nerve and its termination in the posterior occlusor muscle; in this figure the retractor brachia muscle is turned up to expose course of nerve.

Fig. 5. Ganglion of posterior occlusor muscle, greatly enlarged, *idem.*

Fig. 6. Infra-oesophageal ganglia of *T. coreanica.*

Fig. 7. Portion of pallium showing gill ampullae, setae, etc., of *G. pyramidata.*

Fig. 7*a*. Natural size of object showing region from which fig. 7 is drawn.

Fig. 8 to 11. Color markings of the pallium of various species of *Lingulida*. The setae are purposely omitted in these figures except in fig. 9.

Fig. 8. *G. pyramidata.*

Fig. 9. *L. lepidula.*

Fig. 10. *L. anatina.*

Fig. 11. Lingula, species unknown, from Nagasaki.

PLATE 53.

Details of circulation in *Glottidia pyramidata* and *Lingula lepidula*. Arrows indicate direction of currents.

Fig. 1 to 7. *Glottidia pyramidata.*

Fig. 1. Dorsal view showing main and lateral pallial sinuses with lacunae, and coelomic and median sinuses.

Fig. 2. Portion of pallium showing three rows of gill ampullae.

Fig. 3. A single row of gill ampullae, greatly enlarged.

Figs. 4, 5, and 6. Transverse sections through lacune of pallium. Appearance of polygonal cells of endothelium.

Fig. 7. Showing regions of above sections.

Fig. 8 to 12. *Lingula lepidula.*

Fig. 8. Dorsal view. The left brachium is shown with cirri removed.

Figs. 9 and 10. Opening of main pallial sinus and adjacent parts.

Fig. 11. A portion of main pallial sinus showing diverticular lacunae; these appear quite circular in section.

Fig. 12. A single lacune, in section, greatly enlarged. In the drawing of Lingula, at one side, is indicated the region from which figs. 11 and 12 were taken.

Fig. 13. Lateral sinus of *G. pyramidata*; this is figured on the plate laterally.

PLATE 54.

Circulation, blood corpuscles and nephridia of various forms.

Fig. 1. Side view of *G. pyramidata*, showing result of injection of red fluid through peduncular cavity.

Fig. 2. Dorsal view of same. It will be seen that in this experiment the fluid filled the median sinus and the minute vessels of the perivisceral lining, but did not enter the coelomic cavity or the sinuses of the pallium.

Fig. 3. Blood corpuscles of *G. pyramidata.*

Fig. 4. Same of *L. lepidula.*

Fig. 5. Same of *L. anatina.*

Fig. 6. Same of *D. lamellosa.*

Fig. 7. Same of *T. coreanica.*

Fig. 8. Same of *T. septentrionalis.*

Fig. 9. Left nephridium of *G. pyramidata.*

Fig. 10. Greatly enlarged view of portion of nephrostome, *idem.*

Figs. 11, 12, and 13. Nephrostome of *L. lepidula.*

Fig. 14. Nephrostome from the under side, *idem.*

Fig. 14*a*. One fold of nephrostome greatly enlarged showing ciliary ridge, *idem.*

PLATE 55.

Nephridia of various forms.

Fig. 1. Right nephridium of *L. anatina.*

Fig. 2. Greatly enlarged view of nephrostome from below, showing lacunae, *idem.*

Fig. 3. Left nephridium of *D. lamellosa.*

Figs. 4 and 5. Anterior coelomic wall showing terminal portion of nephridial tubes and their external openings, *idem*

Fig. 4. From outside.

Fig. 5. From inside.

Fig. 6. Nephridia from very young *D. lamellosa.*

Fig. 7. Nephridia *in situ* of *T. coreanica.*

Fig. 8. Dorsal section of *T. coreanica,* showing position of nephridia in relation to other parts and their slit-like openings outside.

Fig. 9. Nephridium of *T. coreanica.*

Figs. 10 and 11. Nephridia of *H. psittacea,* showing genital band with accessory vesicle, etc.

Fig. 10*a*. Enlarged view of border of nephrostome, *idem.*

Fig. 11*a*. A sinus from body of nephridium greatly enlarged, *idem.*

PLATE 56.

Nephridia of *Terebratulina septentrionalis* and *Dallina grayii.*

Fig. 1 to 7. *Terebratulina septentrionalis.*

Fig. 1. Left nephridium.

Fig. 2. Right nephridium with divaricator muscles, segment of intestine, ilio-parietal band, etc.

Fig. 2*a*. Nephrostome papillae.

Figs. 2*b* and 2*c*. Appearance of surface of nephridium.

Fig. 3. Nephridium, with genital band, accessory vesicle, etc.

Fig. 4. Peduncular end of young specimen showing nephridia.

Fig. 5. Very young specimen showing nephridia.

Fig. 5*a*. Nephridium greatly enlarged.

Fig. 6. External opening of nephridium, front view.

Fig. 7. Side view of nephridial opening showing nipple-like form.

Fig. 8. Nephridia of *Dallina grayii.*

Fig. 9. Nephridium of last, showing more clearly the crenulated character of nephrostome.

PLATE 57.

Genital products, etc., of various forms.

Fig. 1. Ovaries and stomachal glands of Glottidia.

Fig. 1*a*. Portion of stomachal glands.

Fig. 1*b*. Portion of ovaries.

Fig. 2. Mass of spermaries of Glottidia.

Fig. 3. Mass of spermaries of *L. anatina.*

Fig. 4. Mass of eggs of *L. lepidula.*

Fig. 5. Mass of eggs of Glottidia.

Fig. 5*a* and 5*b*. Eggs in various stages.

Fig. 6. Eggs of *Discinisca stella.*

Fig. 7. Stomach, stomachal glands, and right occlusor muscle of *D. lamellosa* with dio-parietal band turned back to show ovaries arising from it.

Fig. 8. Greatly enlarged view of dio-parietal band from above, figure showing proliferation of genital strands with eggs in masses.

Fig. 9. A group of eggs attached to genital strand, *idem*.

Fig. 10. A group of eggs attached to genital strand, greatly enlarged, *idem*.

Fig. 11. Dorsal and ventral half of pallium of *T. coreanica*, with main pallial sinuses and lacunae filled with eggs; see **39**: 14, for color.

Fig. 11*a*. Terminal lacunae, showing ciliary ridge.

Fig. 12. Masses of eggs, *idem*.

Fig. 13. A single mass of eggs, greatly enlarged, *idem*.

Fig. 14. Side view of portion of mass, *idem*.

Fig. 15. A highly magnified view of a few leaflets filled with eggs, *idem*; see **39**: 13, for color. The yellowish border so characteristic of all membranes associated with genital activity may be seen in the last reference.

PLATE 58.

Genitalia of *Terebratulina septentrionalis*.

Fig. 1. Animal in the act of ovipositing.

Figs. 2 and 3. Small lacunae and spiculae with *corpora lutea*.

Fig. 4. Showing eggs escaping from the lacunae of the pallium, passing through the nephridium, and issuing from the external opening.

Fig. 5. Cluster of eggs from genital band.

Fig. 6. Eggs in lacune.

Fig. 7. Left nephridium with cluster of thread-like spermaries below.

Fig. 7*a*. Sperm threads under a compressor.

Fig. 8. Greatly enlarged view of a few sperm threads.

Figs. 9 and 10. Individual sperm threads showing glandular tip and spindle-shaped termination, with sperm threads; see **39**: 10, for color.

Fig. 11. Lacunae filled with sperm masses.

Fig. 11*a*. Portion of same.

Fig. 11*b*. Spermatozoa.

PLATE 59.

Vesicular organ known as "accessory heart of Hancock," of *Terebratulina septentrionalis*, and central and accessory vesicles of *Terebratalia coreanica*. The accessory vesicle will be designated as genital gland.

Fig. 1 to 8. *Terebratulina septentrionalis*.

Fig. 1. Genital gland springing from genital band with supplementary vesicles near.

Fig. 1*a*. Enlarged view of surface showing spermatoblasts.

Fig. 2. Genital gland more developed with glandular growth at base.

Fig. 3. Genital gland with supplementary gland at side.

Fig. 3*a*. Much enlarged view of same.

Fig. 4. Genital gland arising from slender stalk with glandular outgrowths on surface.

Figs. 5, 6, and 7. Genital glands in various stages of development.

Fig. 8. Portion of genital band thickened and strongly ciliated.

Fig. 9 to 13. *Terebratalia coreanica*.

Fig. 9. Stomach with so-called heart and genital glands at end of main pallial sinus, with glandular cord connecting them with the so-called heart; see **39**: 12, for color.

Fig. 10. So-called heart.

Fig. 11. Another view of same organ slightly compressed.

Figs. 12 and 13. Different views of genital gland.

PLATE 60.

External glands of *Terebratulina septentrionalis.*

Fig. 1. Shells thrown widely apart rupturing anterior coelomic wall, showing brachia, position of nephridia and relation of external glands to nephridial openings.

Fig. 2. Another view of nephridia with external glands.

Fig. 3. External gland compressed with glandular particles forced out.

Fig. 4. Greatly enlarged view of lobule of external gland showing ciliated epithelium.

Fig. 5. External gland showing spiculae on surface.

Fig. 6. Nephridia with external glands surrounding their terminations.

Fig. 7. Greatly enlarged view of right nephridial tube with external gland.

Fig. 8. Tubular portion of nephridia ensheathed by external gland.

Fig. 9. Another view of nephridium surrounded by lobules of external gland.

Figs. 10 and 11. External glands.

Fig. 12. Ventral view of anterior wall of coelomic cavity showing prominent character of external glands with azygos process between.

Fig. 13. Longitudinal section of *T. septentrionalis*, showing position of external glands projecting into pallial cavity.

PLATE 61.

Early stages of various forms.

Fig. 1. Lingula, species unknown, from Nagasaki.

Figs. 2, 3, and 4. *Discinisca stella.*

Fig. 5 to 12. *D. lamellosa.*

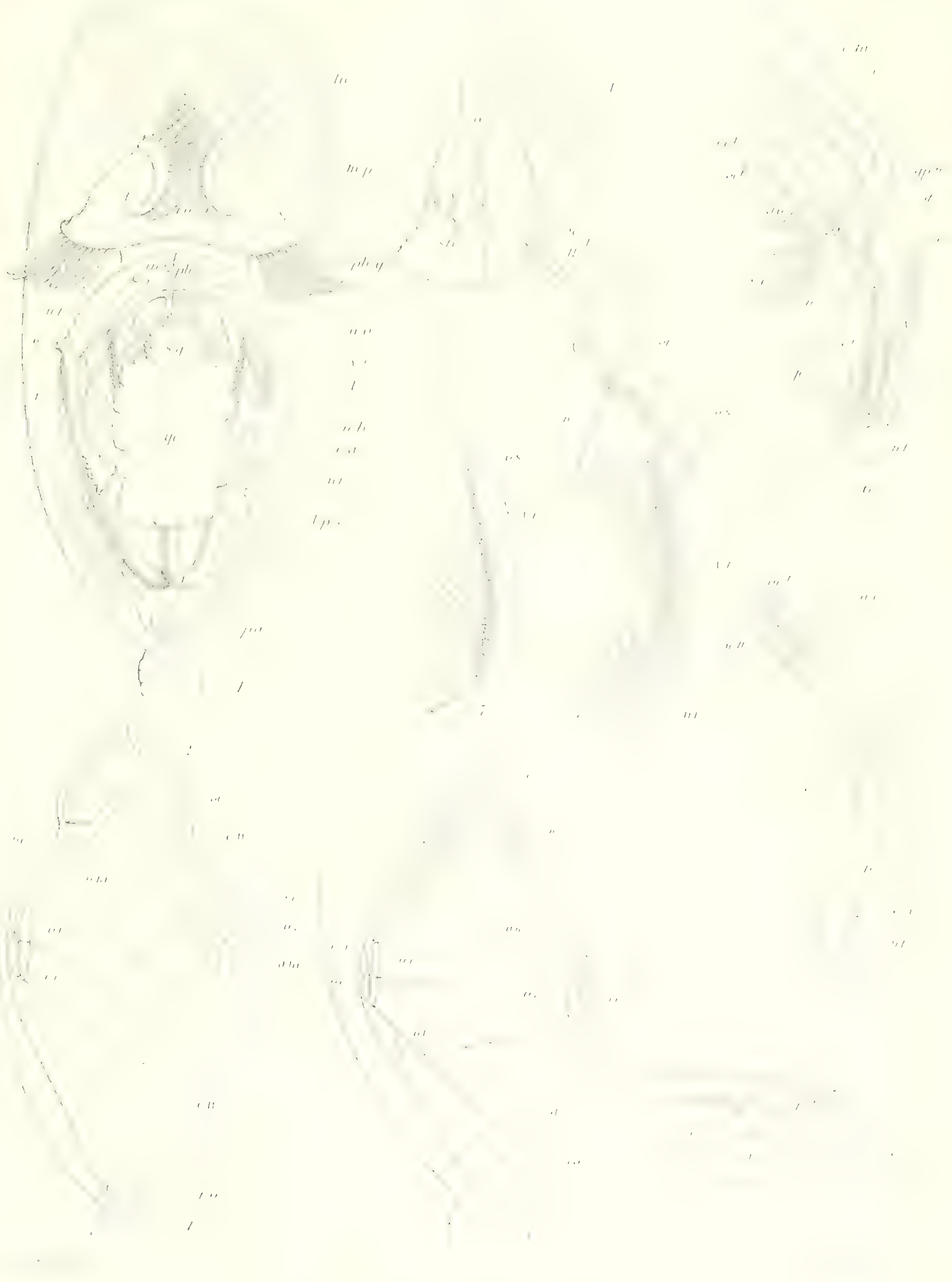
Fig. 13 to 16. Various stages of *T. septentrionalis*, reproduced from the author's memoir on early stages of this species.

Fig. 17. *Hemithyris psittacea.* The natural size is indicated by the small outline.

Printed, July, 1902.

MORSE ON LIVING BRACHIOPODA

ep
1
11
12a



pcd
ap
sta
ol
pbl
ap

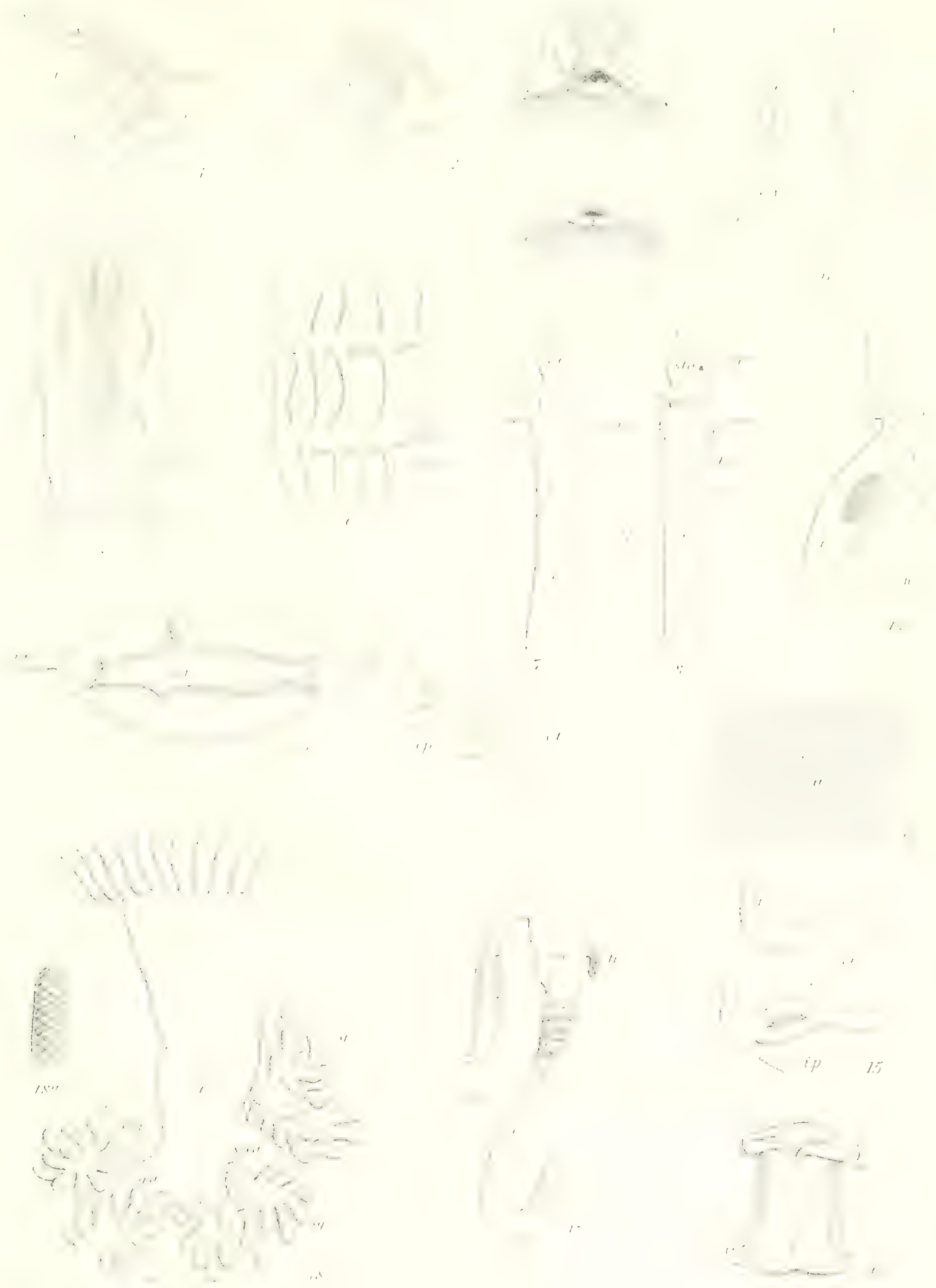
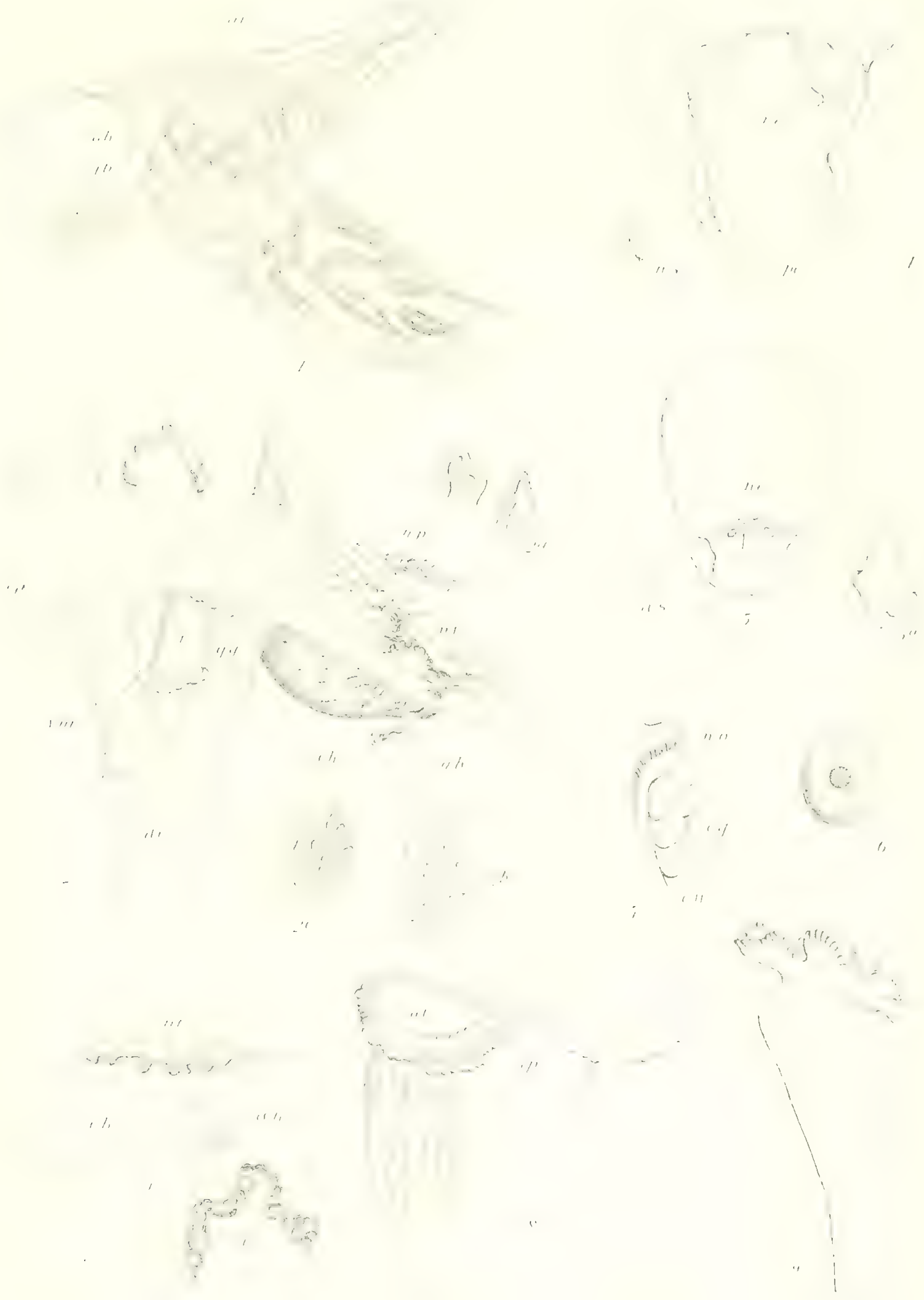

ip
15

PLATE 51

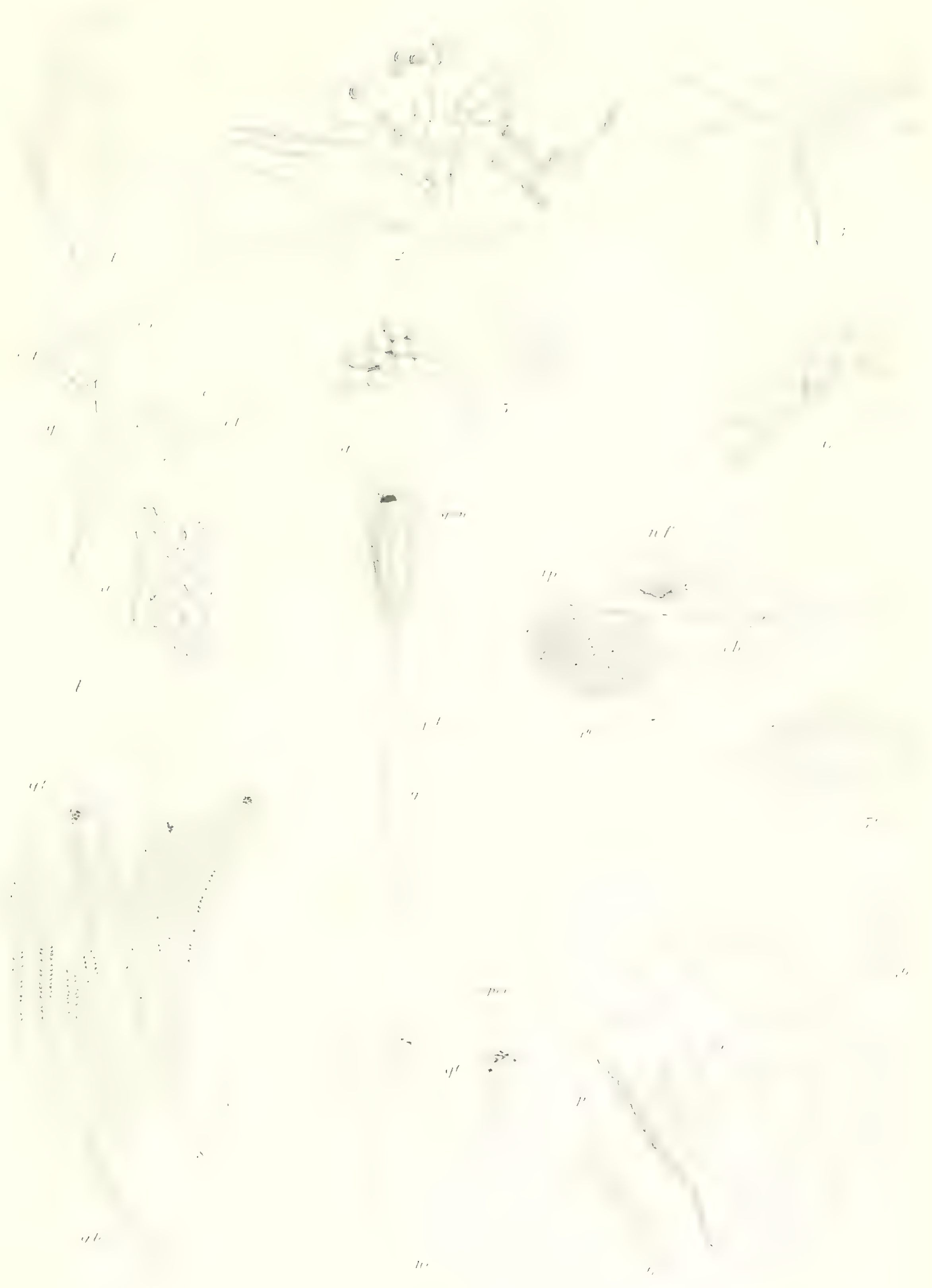
dpm
po
gpa

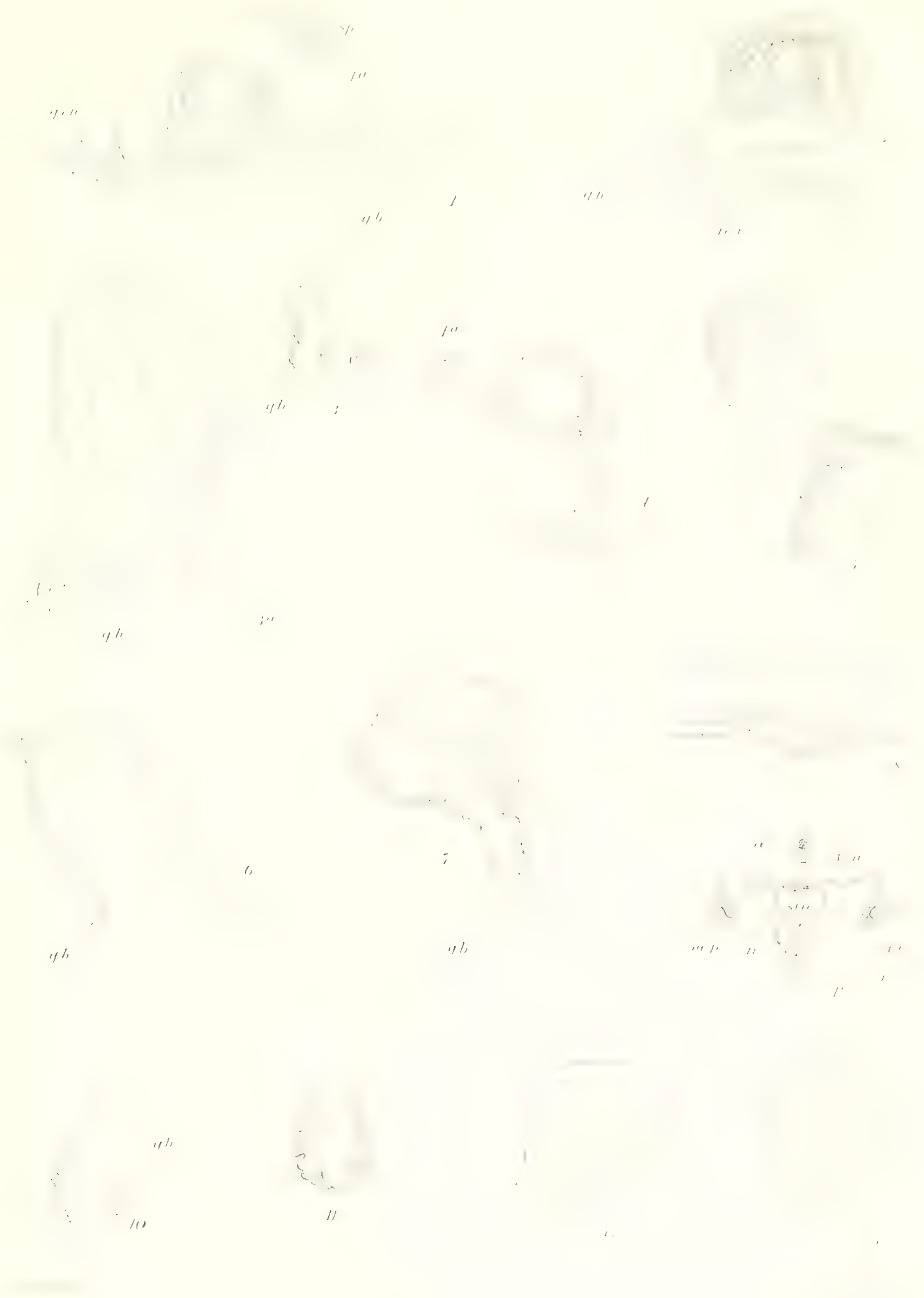
MORSE ON LIVING BRACHIOPODA

qb
ah
no
lo
dm
no
no
ub
ip
mo
ub



Morse on Living Brach





MORSE ON LIVING BRACHIOPODA

9. THE SKELETAL SYSTEM OF NECTURUS MACULATUS Rafinesque.

BY HARRIS HAWTHORNE WILDER, PH. D.

(Read February 19, 1902.)

INTRODUCTION.

IN view of Gaupp's recent revision of Die Anatomie des Frosches, Professor von Bardeleben says, "Es wäre im Interesse einer besseren Fundamentirung der vergleichenden Anatomie höchst wünschenswert, wenn bald zu den wenigen ausführlichen Monographien von Wirbeltieren einige neue, z. B., je eines Selachiers, Ganoiden, Teleostiers . . . . eines Urodelen . . . . einiger Reptile und niederen Säuger, besonders Insectivoren, kämen. . . . Wer wagt es?" The following paper is an attempt to carry out the suggestion of the above quotation as far as it concerns a Urodele; and it is hoped that, as occasion allows, papers upon the other systems of Necturus may be added to this and thus gradually complete a monograph upon the anatomy of a typical tailed amphibian.

In the selection of Necturus to serve as a type, I have been guided by several reasons, mostly of a practical nature. *Necturus maculatus* is probably the most abundant and widely distributed Perennibranch in the world, and owing to this fact, as well as to its large size, is employed as universally in American laboratories, as is the *Salamandra maculosa* in Europe. This exploitation of the species as a laboratory animal has led to the development of means for its capture in quantity for such purposes, and it is thus by no means so uncommon an object of study in the laboratories of Europe as it was a few years ago.[1]

Anatomically and structurally considered, the choice of an animal to represent the Urodela should be either that of a highly specialized one, thus emphasizing those characters which are essentially Urodelan; or that of one taken from the most primitive group, which would have the two advantages of showing each organ in its simplest condition, and of suggesting the phylogenetic origin and relationship of the entire order.

Granting that the second of the above alternatives has the most in its favor, the choice would be limited to one of the *Proteidae*, a family represented by three generic groups, which are partially or wholly subterranean in their habits and thus modified in various degrees to conform to this environment. Proteus is an inhabitant of certain caves in Austria, and shows, among other troglodytic characters, reduction of eyes, loss of pigment, and a pronounced attenuation of body and limb, the latter combined with a loss of toes. These aberrant characteristics are still more marked in the recently discovered Typhlomolge, which occurs in a subterranean river in the state of Texas. The third and last member of the group, Necturus, occurs in the Great Lakes and other open waters, and, corresponding to its freer life, shows the least modification. It remains by day beneath stones or in subterranean burrows constructed by itself in the mud, and becomes active at night, swimming through the water in search of prey. Its body and legs are robust, and do not show the slender proportions seen in Proteus and Typhlomolge. Its eyes, though small, are functional, and it is well pigmented, especially above. It is thus at the same time a representative of the lowest group of Urodeles, and one not extremely modified.

---

[1] Necturus is supplied at present at most of the American universities at $10.00 per hundred, and although just at present there is an attempt being made by dealers to advance the price, especially of those exported to Europe, such conditions cannot last long.

The genus Necturus is exclusively North American and includes but one common species, *N. maculatus* Raf., although the series of synonyms, as well as some variability of marking, have combined to give the general impression that there is a large number.

Aside from *N. maculatus* Raf., Cope enumerates a second species, *N. punctatus* Gibbes, of rare occurrence and found only in the waters of North and South Carolina.

Necturus maculatus, the subject of this memoir, is a widely distributed form and occurs in abundance in the Great Lakes and their tributaries, and throughout the entire Mississippi valley, as well as in many of the river systems of the Atlantic slope, and those flowing into the Gulf of Mexico. Its abundance and extensive distribution have led the United States government to conduct experiments relative to its introduction as a "food fish," thus far with satisfactory results. In form and appearance it is similar to that of a larval salamandrid, and is subcylindrical, body slightly and head markedly depressed, with three large and bushy external gills upon each side, having two gill slits between them, and with four decidedly robust legs, each with four toes. The tail, which does not exceed half the length of the body, is compressed and surrounded dorsally, caudally, and ventrally by a caudal fin, rounded in outline at the tip. Sexually mature adults seem to be fairly constant in size, varying in total length between about 27 cm. and 34 cm.

The color markings of the integument are due to scattered pigment cells, the variations in the frequency and size of which result in the formation of all possible shades between no color at all and dense black spots. As these cells are very large, and in most places evident to the unaided eye, the principle is seen upon close inspection to be similar to that of a modern half tone illustration, which a careful scrutiny resolves into a series of black dots, although in the latter case the darker shades are due to increased size, and in the former to an increased number of the elements involved. The ground color of the skin, as may be seen on the ventral side, which is mainly free from pigment, is yellowish or pinkish, but over the sides and back varying degrees of pigmentation produce different shades of slate color, in places with a distinct bluish or purplish tint. The deepest pigmentation is that of the dorsal side where certain densely pigmented areas form irregularly rounded black spots upon a bluish-slate background, thus suggesting the specific name of "*maculatus*."[1]

The skeleton consists of several independently separable portions and, like that of other Urodeles, contains a large amount of unossified hyaline cartilage. By far the largest portion consists of the vertebral column, the skull, to which is attached the hyobranchial complex, and the posterior extremities, which are attached by the ilia to a single sacral vertebra. The two halves of the shoulder girdle are free from one another and from the rest of the skeleton, and they, with their corresponding free limbs, form two distinct skeletal parts. The remaining skeletal elements are the nasal and optic capsules, the two laryngo-tracheal cartilages, and the series of rudimentary sternebra which lie in the mid-ventral thoracic region. All of these latter parts are wholly cartilaginous and entirely disconnected from other parts of the skeleton.

In arranging the descriptive material of this memoir, the above practical division of the skeleton has been taken into consideration as well as the more usual morphological one, and it has seemed best to arrange the subject in the order following. In this the vertebral column will be first treated, together with the ribs and sternum. The visceral arches and the free sense capsules will be treated with the skull, and the limbs and their girdles will appear last. This brings the parts together in their topographical relationships and will be found more practical than a wholly morphological division.

THE VERTEBRAL COLUMN.

General Description.

The vertebral column, as is the case with fishes, shows little regional differentiation, since the limbs are too small and weak either to modify the motions of the trunk by the muscles attached to them, or to bring their places of attachment into prominence as points of leverage or support. The only gain in this respect over the condition seen in fishes is the direct attachment of the pelvic girdle, which by the medium of a specialized pair of ribs, becomes articulated to a single vertebra, usually the 19th. This vertebra, the sacral, lies naturally in the cloacal region and it seems a matter of doubt whether, as in higher forms, to consider it the boundary between the trunk and the tail, or whether as in fishes, to limit the latter region to those vertebrae which bear closed haemal arches, the first of which is usually the fourth vertebra posterior to the sacral one, *i. e.*, the 23d. The first of these alternatives seems the more natural and open to the fewest objections, for, while it places the first few caudal vertebrae in the same list structurally with those of the trunk, from which, indeed, they are practically indistinguishable, it avoids the equally great embarrassment of leaving the same number as a nameless and anomalous group intervening between the sacral and caudal regions, a relationship unlike anything occurring elsewhere among vertebrates.

---

[1] Just as this manuscript leaves my hands, I have received from Mr. Alexander Nielson, of [illegible] an extensive dealer in Necturus, a specimen having a totally different coloring from the [illegible]. Mr. [illegible] has caught thousands of specimens, writes that it is the first of the kind he has ever seen. [illegible] men is a light reddish buff, with no suggestion of the usual dark slate color. The back is covered with dark brown spots, smaller than in the normal forms. In form and size it closely resembles the common species.

The statements given above, that the two vertebrae which have a definite distinction, the sacrum and the "first haemal arch vertebra," are usually the 19th and 23d respectively, suggest variation in this order, a matter which has been made the subject of papers by G. H. Parker ('**96**) and Bumpus ('**97**), and has been referred to by Waite ('**97**).

Regarding the sacral vertebra, according to the first two authors it was the 19th in 65% of 127 specimens examined, the 20th in 27% and in the remaining 8% it was placed "obliquely," that is, with an attachment to the 19th vertebra upon one side and the 20th upon the other. This obliquity is usually sinistro-dextral, *i. e.*, with the left sacral rib in advance of the right (left, 19th; right, 20th). Out of eight such oblique specimens examined by Bumpus, seven were sinistro-dextral, and only one dextro-sinistral. Parker's two specimens were both sinistro-dextral.

Waite describes three oblique specimens, which show for the most part additional abnormalities. In one of these the right sacral rib was on the 19th vertebra and the left on the 20th, thus making the direction dextro-sinistral. In the other two cases the right rib was on the 18th, a case not found by the other authors named, and the left on the 19th, again dextro-sinistral.

Waite also figures a case with two normal sacral ribs on the 19th vertebra, and an additional smaller rib upon the right side of the 20th, also attached to the ilium.

A similar variation occurs in the position of the 1st haemal arch, although a careful comparison by Bumpus has shown that variation here is entirely independent of that of the sacral vertebra. Out of 98 specimens examined with reference to this, the 1st haemal arch was borne on the 22d vertebra in 11 specimens, on the 23d in 82, and on the 24th in 5.

The variation in the total number of vertebrae, which is considerable, is seen to be mainly that of the caudal region, as it has been shown that there is a variation of but two vertebrae at the sacrum, and but three at the first haemal arch. The results of counting the vertebrae in 100 specimens are expressed by Bumpus in the following table: —

No. of vertebrae.	No. of specimens.
43	2
44	9
45	21
46	18
47	14
48	16
49	11
50	5
51	4
	100

By this it will be seen that the average total number is 45 or 46.

A Typical Vertebra.

In order to understand the structure of the separate vertebrae, any trunk vertebra except one of the first two or three may be selected as a type and its parts studied in detail, after which the differences seen in other regions may be noted, and a few special vertebrae selected as worthy of individual study. The 16th vertebra has been selected for this purpose, and four views are given of it in text figures 1–4. These figures were drawn from a dried vertebra prepared by maceration in caustic potash and hence lack the cartilaginous portions and other related soft parts referred to in the text.

This vertebra consists primarily of a ventrally situated centrum or body; a neural arch, the dorsal aspect of which is broadened out into a broad, flat plate; and upon each side a complicated transverse process directed backwards and bearing a short rib which articulates with it in two places.

The centrum is in the form of a slender hour glass, its ends marked by very deep cup-shaped depressions, thus making the entire vertebra con-

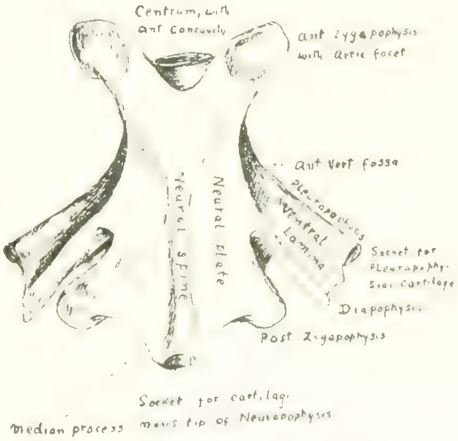

Centrum, with ant concavity
ant zygapophysis with artic facet
Ant Vert fossa
Pleurapophysis
Ventral Lamina
Neural spine
Neural plate
Socket for Pleurapophysial cartilage
Diapophysis
Post Zygapophysis
Socket for cartilaginous tip of Neurapophysis
median process

Fig. 1. 16th vertebra, dorsal aspect. × 3 spicuously amphicoelous. In the recent state these depressions are filled in with portions of the original notochord which become restricted to these intervertebral segments by the development of the osseous vertebrae. Corresponding to the shape of the space included by two approximated ends of vertebrae, these notochordal segments are in the shape of two cones placed base to base, the place where the two bases meet being the line of separation between the two vertebrae involved.

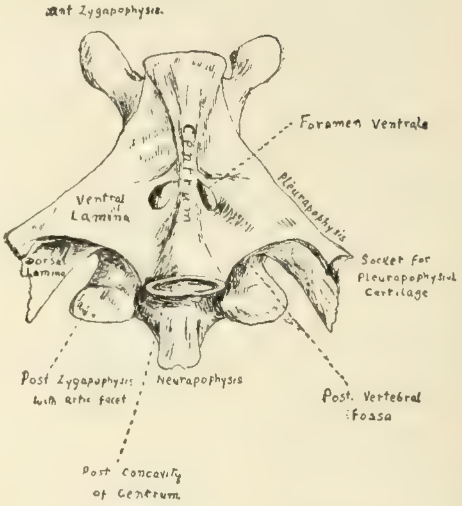


Fig. 2. 16th vertebra ; ventral aspect. × 3.

The neural arch is much flattened dorsally, and its sides, the neural laminae, become so much obscured by fusions with the elements of the transverse process that they are seen distinctly only when the vertebra is viewed from one end. The main bulk of the arch consists of a flat neural plate, which in a dorsal view of the vertebra nearly conceals the rest. This plate is approximately a rectangle with sides a little incurved. Anteriorly its corners become prolonged into a pair of rounded anterior zygapophyses, and posteriorly it develops a pair of somewhat similarly shaped posterior zygapophyses, between which extends a short, median process. As the posterior zygapophyses of each vertebra overlap the anterior ones of the next succeeding, the articular surfaces of the former lie upon the ventral, and those of the latter upon the dorsal aspect. At the blunt posterior point of the posteriorly directed median process, there is a small cup-shaped depression filled, in the recent state, with a nodule of cartilage which forms the tip of the neural spine, the osseous continuation of which extends along the median line of the neural plate, becoming obsolete anteriorly.

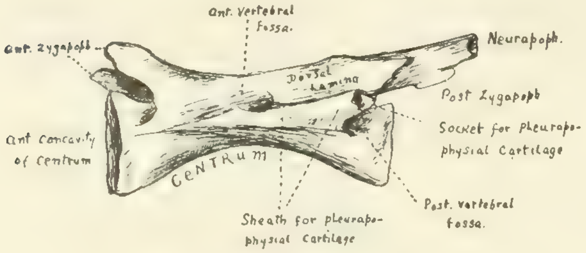


Fig. 3. 16th vertebra ; left lateral aspect. × 4.

The term "transverse process" is a convenient name by which to distinguish certain composite and irregular masses placed upon either side of the centrum and bearing the proximally forked ribs. Each transverse process consists essentially of two cartilaginous rods, dorsal and ventral, encased in an irregular bony mass. Of these two rods, the dorsal one, the diapophysis, proceeds from the side of the neural arch, while the ventral one, the pleurapophysis, is associated with the centrum. The investing bony mass is formed secondarily about these rods by periostosis and consists essentially of two simple investing sheaths and two flattened laminae, of which one is vertical and dorsal, connecting the two sheaths, and the other horizontal and ventral, applied to the ventral side of the pleurapophysial sheath and spreading out proximally over nearly the entire length of the centrum, with which it becomes fused. This latter lamina is perforated by the ventral foramen, situated immediately posterior to the pleurapophysis and transmitting the collateral vertebral vessels. As the dorsal lamina meets the ventral one nearly at right angles, they form with the side of the centrum, two fossae, the anterior and the posterior vertebral fossae. The posterior fossa is much the deeper and communicates with the region ventral to the vertebral column by means of the ventral foramen just mentioned.

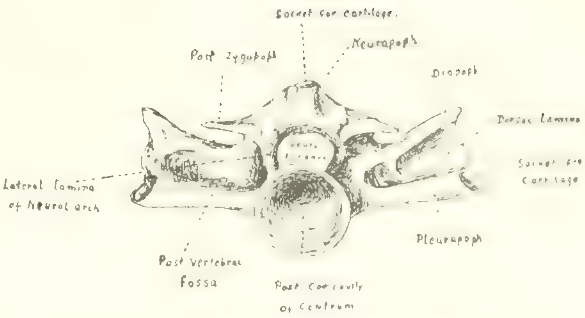


Fig. 4. 16th vertebra, posterior end view. × 3.

In the larva the cartilaginous diapophysis and pleurapophysis are directly continuous proximally with a lateral mass, the "rib bearer" (Rippenträger) of Göppert, while distally they unite to form the cartilaginous rib, the whole mass being at this time a continuous piece. The process of ossification within and around the rib bearer and the sides of the vertebrae, and especially the growth of the osseous sheaths about these rods, gradually cut them off from one another and restrict them proximally into tapering points, so that in a macerated adult vertebra, from which all the cartilage has been removed, the moulds of the parts in question are seen as very deep and conical pockets.

Later ossification separates the free rib from the encasing sheaths of the transverse process, and joints are thus formed between the two bodies. The part of the rib thus segmented from the diapophysis forms the tubercular process and the part once in connection with the pleurapophysis becomes the capitular process, both processes retaining throughout life an articular connection with the rods from which they originally separated.

Embryological investigation has rendered it probable that the pleurapophysis and its associated capitular head represent the primary condition, and that the cartilage of the rib bearer becomes dorsally extended for increase of support, developing later the secondary or tubercular attachment. Göppert has shown this secondary growth of the tubercular connection in the case of Triton and some other Urodeles, a growth which proceeds from the ribs and follows along a line of connective tissue until it reaches the rib bearer at its dorsal prolongation, applied to the side of the neural arch. As he expresses it in his summary, "Die dorsale Spange ist ein verlängertes Tuberculum, das im Dienst einer ausgiebigeren Befestigung der Rippe steht." Unfortunately he fails to find this dorsal connection in Necturus, and states that "der dorsale Theil des Querfortsatzes tritt nicht so deutlich als ein Balken hervor wie bei Salamandra und entbehrt auch hier der distalen Höhlung, da die dorsale Rippenspange den direkten Anschluss an den Querfortsatz nicht erreicht."

As shown below, and in several of my figures, this "distale Höhlung" at the tubercular articulation of the transverse process is often very evident, and through the medium of the enclosed cartilaginous rod, articulates with the tubercular process of the free rib. Göppert's description ('**96**, p. 398) of the condition in Salamandra corresponds so completely with that of the adult Necturus that it could well be substituted for the description given in this work. The "Abweichungen" which he finds in Necturus do not exist.

A summary of the main features of a typical vertebra and its relations to other parts of the skeleton may be given as follows: —

1. Osseous elements. Centrum; neural arch, including dorsal plate and lateral laminae; transverse process, including sheaths of rib bearers, and the associated dorsal and ventral laminae.

2. Cartilages and other soft parts. Two pairs of lateral rods or rib bearers; a neural spine; intervertebral notochordal cones.

3. Articular surfaces. Two for the centrum; two anterior and two posterior zygapophyses; two tubercular and two capitular articulations for the corresponding heads of the ribs.

Comparison with Other Vertebrae.

A study of the separate features brought out in the above description, as they occur in the rest of the vertebral column, yields the following results. These, for the sake of brevity, are expressed somewhat in the form of a table in which a few obvious abbreviations are employed. Thus the vertebrae are expressed by consecutive numbers, beginning the enumeration with the atlas, which is 1; S is the sacral vertebra (19 or 20), and H is the first one bearing a haemal arch (22 to 24).

Neural and haemal spines. — The neural spine forms a prominent ridge in 1; somewhat depressed and rounded at the end in 2. The neural spine of 3 shows the maximum of size in the trunk vertebrae and is here the most erect, *i. e.*, makes the greatest angle with the longitudinal axis of the vertebra. From there as far as S, it is gradually smaller and more depressed. After S it becomes again larger and more erect, so that the spine of 21 is about equal to that of 3, and that of 22 surpasses it. It rapidly lengthens as far as 26 to 27, where it reaches its maximum of length and is about equal to the haemal spine; from then on, both neural and haemal spines become gradually reduced as the vertebrae diminish in size.

A haemal spine appears suddenly on the 22d to 24th vertebra, usually the 23d, an indication of it sometimes being found upon the previous vertebra in the form of a thin bony bridge which stretches across the ventral face of the vertebra from the outer angle of the transverse process to the centrum, thus covering the posterior portion of the ventral lamina. In one case noted, the vertebra just anterior to H bore upon one side a slender process, 4 to 5 mm. long, evidently representing an incomplete haemal arch. The first haemal spine is of about the maximum size, and, after three or four vertebrae in which this size is maintained, the haemal spines begin to diminish with the gradual reduction of the vertebrae, as in the case of the neural spines. The neural and haemal spines of the same vertebrae closely resemble one another, but, in the first few vertebrae that possess both, the former take a slightly more erect position while the latter lie more nearly parallel to the axis of the vertebrae. Towards the end of the tail both neural and haemal spines sometimes appear bifurcated at the tip, or even double as far as their base. In a given vertebra this may affect either spine alone or both spines.

Zygapophyses. — In 1, the anterior zygapophyses are wanting and the posterior are near together. From 2 to S both sets are divergent and almost identical, save that the entire vertebrae at about 15 to 17 are a little wider than elsewhere and hence the zygapophyses are here farther apart. After S the vertebrae rapidly become narrow, and, beginning with H, both sets approach very near together and are reduced in size. They become obsolete at about 26, beyond which the vertebrae articulate solely by means of the vertebral centra.

Ventral foramina. — These do not appear in the three anterior vertebrae and are usually of small size in 4. From then on, as far as H, there is usually a pair in each vertebra, although occasionally the foramen of one side may be converted into a notch by a deficiency in the ventral lamina. In H, where the roots of the haemal spine form thin laminae lying over the region of these foramina, openings occur not only in the ventral laminae as usual, but also in the laminae connected with the haemal spine, and the two sets of foramina are accurately superimposed. Beyond H the reduction of the entire transverse process renders the ventral foramina unnecessary, but in the two or three vertebrae succeeding H the new foramina through the base of the haemal spine may be present, although usually appearing upon but one side.

Transverse processes. — These processes, quite rudimentary in 1, are represented in 2 by the dorsal lamina alone, while the ventral lamina appears but slightly indicated by a curving in of the ventral margin of the former. A continuation of this method produces in 3 a fair indication of a ventral lamina, which in 4 has become of normal size and appearance. In vertebra 2 to 7, approximately, the dorsal laminae are set perpendicularly, beyond which they grow more and more oblique. In the sacral vertebra they become again nearly perpendicular, beyond which they rapidly become obsolete but remain more nearly perpendicular. As they degenerate they separate into two portions, a dorsal and a ventral, corresponding to the diapophysis and pleurapophysis (Göppert's "Balken"). This division occurs at approximately the 25th vertebra, after which the dorsal or tubercular portion disappears in 2 to 3 more vertebrae, while the ventral or capitular portion persists for a few vertebrae farther.

Attachment of ribs. — As shown above, the ribs are bifurcated at their proximal ends, the two being known as the dorsal or tubercular and the ventral or capitular attachments. These relations of the soft parts are plainly indicated in dried specimens by the presence and relative development of the sheaths, the laminae of which furnish a set of moulds giving the exact condition of the cartilages, and thus the following items, although obtained for the most part from dried specimens, will doubtless be found to be wholly reliable. Vertebra 1 is entirely without ribs. In 2, 3, and 4, both tubercular and capitular ends of the ribs are of large caliber and both are attached to cartilaginous rods. In 2 the capitular sheath is exceedingly small and the tubercular one a little larger. In 3 the tubercular sheath is quite large and the capitular one a little smaller, and in 4 both are large, the capitular sheath being slightly in excess of the other. From 5 to 8 the capitular sheath is always present but there is no distinct tubercular one, this attachment being one of simple osseous contact. In the sacral vertebra there are two sheaths, one for each attachment. They are of about equal size and are larger than in any other vertebra. These two attachments of the sacral rib are figured and described by Göppert (**'96**, p. 402), but, since he has failed to find them in the other vertebrae and has even stated that a tubercular attachment does not exist, he is under the necessity of accounting for them in some other way. This he does by describing a process (Höcker) which grows out of the side of the rib bearer, and "dient der Befestigung der kurzen oberen Spange der Sakralrippe." Although these words are noncommittal, the implication is, that this "Höcker" and the connection thus formed are a new formation and not homologous with the dorsal or tubercular connection. This leads to the inevitable conclusion that the dorsal or tubercular connections of the sacral ribs are not homologous with those of the others, a conclusion which a moment's consideration of an entire adult skeleton would render invalid. The vertebrae which intervene between the true sacral vertebra and the one bearing the first haemal arch, vary considerably in their relation to costal elements. The first of these vertebrae in many cases bears a small pointed rib with a capitular attachment alone, but this seems to be more usual in cases in which the sacral vertebra is the 19th. In one such case with the first haemal arch upon the 22d vertebra, the 20th bore small ribs and upon the 21st appeared very minute capitular sockets, which, as this was a macerated specimen, might have originally borne rib rudiments. There seems to be much variation in these as well as in other particulars in this very variable region, but the specimens examined have been too few in number to give any general conclusions.

Study of Special Vertebrae.

Atlas.—The main characteristics are the reduction in total length to about one half that of a normal trunk vertebra, the peculiar shape of the centrum, the rudimentary condition of the transverse process, and the conspicuous and projecting neural arch. The posterior end of the centrum is normal but anteriorly it broadens rapidly to form a wide wedge, the base of which is directed forwards and bears the two condyles. These are slightly concave, elliptical surfaces, inclined a little outward, and meeting in the median line where a small but conspicuous tubercle is formed that fits into a space upon the ventral side of the skull between the two exoccipitals. The ventral aspect of the centrum is somewhat hollowed and a little roughened for muscular attachment, a peculiarity shared by the 2d vertebra. The neural arch is large and conspicuous. Its sides are flattened and obliquely set, and it ends in the mid-dorsal line in a rounded edge or keel, the posterior end of which bears a small socket for the cartilaginous tip of the neural spine, as in other vertebrae. The two posterior zygapophyses are large and heavy. The transverse processes are rudimentary and very variable, even upon the two sides of the same vertebra. Their most constant parts are a usually bifurcated piece projecting obliquely backwards in the same position as, and probably homologous with, the dorsal lamina of the succeeding vertebrae; and a much shorter spine, placed ventral to this and also projecting backwards. The larger process is pierced by an obliquely directed foramen which communicates with the neural canal and transmits the internal carotid artery and the first pair of spinal nerves.[1] Between this process and the short ventral spine there is a narrow but very deep fossa. By the bifurcation of the original transverse process and the addition of the spine ventral to it, there are formed three backwardly directed processes which are very variable in their mutual relations. Occasionally all three will be distinct and of about the same size, but usually the ventral spine is much smaller than the other two. There may also be varying degrees of bifurcation of the genuine transverse process, or it may present one or more small processes in addition to the usual three.

---

[1] Hoffmann suggests that the phenomenon of a pair of spinal nerves boring through the substance of a vertebra, in an animal in which the nerve exits are normally intervertebral, is an indication that the "atlas" really represents two fused vertebrae, the line of separation being marked by the nerve and its foramen.

Vertebra bearing the first haemal arch. — This is normally the 23d in the series, but it may be the 22d or even frequently the 24th. After the sacrum, the neural plates rapidly narrow, and, by the time the vertebra in question is reached, this part has become about as narrow as the base of the neural spine, so that the latter appears in direct continuation with it, the posterior zygapophyses appearing as lateral processes borne upon the sides of the spine. This increase of the apparent length of the neural spine renders it strikingly similar to the haemal spine, and thus is seen the first suggestion of that dorso-ventral bilaterality which becomes so marked in the more posterior caudal vertebrae. The transverse process is thin and poorly developed, and the occasional bifurcation of its free end gives an indication of its division into tubercular and capitular portions as seen in the vertebrae immediately posterior to this. The haemal arch, which is a new element and thus gives distinction to this and the following vertebrae, begins as a pair of low, thin ridges springing from the ventral side of the centrum and uniting across the mid-ventral line near the posterior limit of the vertebra in such a way as to frame in a haemal foramen just ventral to the centrum, which, with the foramina of the succeeding vertebrae, forms the haemal canal. The ventral laminae are perforated as usual by the two ventral foramina, and, as they are nearly covered by the two ridges that form the roots of the haemal arch, a pair of foramina occurs also in these latter opposite the usual ones. In most instances the first haemal arch appears, as it were, suddenly and perfectly developed, and the vertebra immediately preceding the one that bears it usually shows no suggestion of such a structure. Occasionally, however, a rudiment of the foot or root of the arch appears upon one or both sides of the previous vertebra in the form of a thin plate lying parallel to the ventral lamina, and extended across from centrum to outer end of the transverse process, and, in one instance observed, a slender haemal process appeared upon the left side, which projected back over the following vertebra and plainly represented one side of a rudimentary haemal arch. There was no trace of this upon the other side.

The caudal vertebrae posterior to the above, with especial reference to the terminal ones. — The most conspicuous characteristic of the caudal vertebrae posterior to the above is the presence of nearly equal neural and haemal arches running out into long spines with their free ends pointed obliquely backwards. The reduction of the transverse process, which begins just posterior to the sacrum, progresses rapidly after passing the first haemal arch. The process first becomes divided into its two portions, the dorsal one of which survives but two or three vertebrae, while the ventral one continues for two or three more. *Pari passu* with the loss of the transverse processes, the zygapophyses become reduced and finally disappear. With the loss of these lateral elements the vertebrae become narrowed from side to side, and, as this appearance is further increased by the great extension of neural and haemal arches and spines, the entire column becomes strongly compressed laterally, thus corresponding to the change in external form which is so apparent in the living animal. In this more characteristically caudal region (*circa* between 28 to 40) the hour glass shape of the centra becomes more apparent and in the reduction which follows towards the tip, this element becomes more and more conspicuous as the main portion of the vertebrae. Thus, after about the 40th vertebra, rapid reductions take place in the arches, both neural and haemal, and the terminal one or two vertebrae consist of centra alone, the posterior end of the final one being rounded and without the characteristic cup. In this loss of arches it seems that the neural arch disappears first, as in all the cases examined several of the last vertebrae consisted of body and haemal arch alone, but the specimens examined were too few in number to establish this as a law. From about the point at which the vertebrae first become laterally compressed, or more exactly, after the loss of the zygapophyses, there is shown an almost complete dorso-ventral bilateral symmetry, so that in an isolated vertebra it becomes extremely hard to distinguish between the neural and haemal arches. There is, however, a slight difference which, though difficult of formulation, may be perceived after a little study and seems to consist mainly in a some-

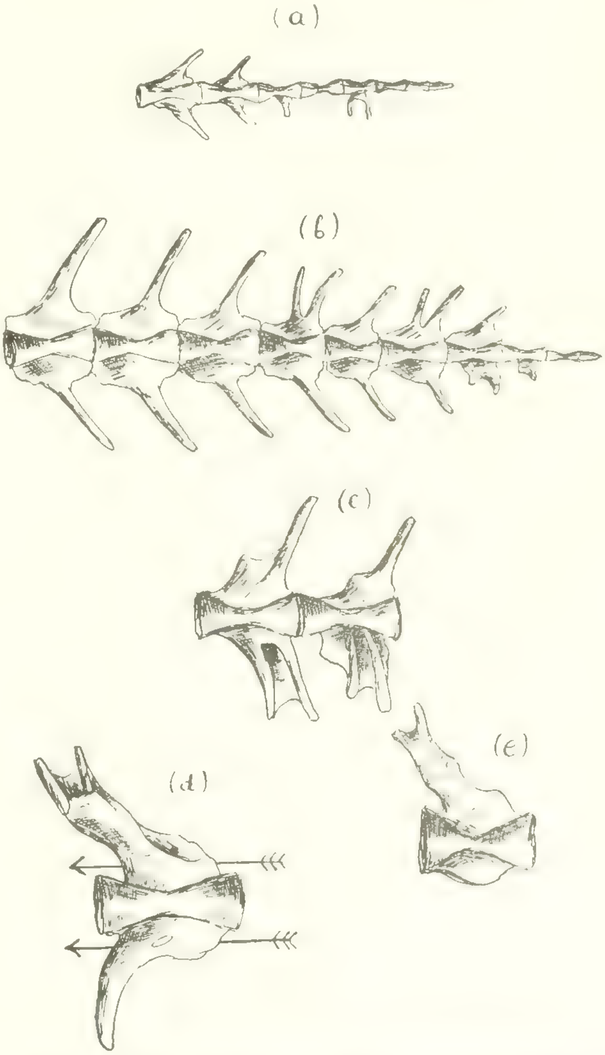


Fig. 5. Caudal vertebrae. (a) and (b) two examples of terminal vertebrae; (c) instances of double haemal spines; (d) and (e) two successive vertebrae in the same series showing doubling of neural spines. The arrows in (d) pass through the neural and haemal canals.

what greater size of the neural canal in comparison with the haemal, and a consequent greater height of the anterior portion of the neural arch, which in this region becomes prolonged and tubular.

A common phenomenon in these last caudal vertebrae, beyond about the 38th, is an antero-posterior bifurcation or doubling of either the neural or the haemal spines or both. Frequent examples of this are noticed in the accompanying figure (fig. 5), in which appear several grades of this malformation, from a bifurcation of the free end to what seems to be a complete doubling of the spine. This phenomenon is referred to by Bumpus ('97) and figured in some of his radiograph illustrations.

Sternum.

The several cartilaginous rudiments which represent this part in Necturus are somewhat difficult of detection and thus entirely escaped the attention of the earlier investigators. They consist of a number of thin cartilages found in several successive myocommata of the pectoral region and confined mainly to the area covered by the overlapping epicoracoids. As will be seen by text figure 6, which represents the sternal elements of six normal individuals, the cartilaginous pieces show great individual difference in shape and size, and are capable of some variation in the myocommata involved. The largest segmental portion or sternebrum is that of the 4th myocomma which is in general an irregularly triangular or often bat-shaped piece. It lies just posterior to the epicoracoids, in the angle formed by their overlapping edges, and is sufficiently large and superficial to give rise to a part of the fibers of the pectoralis muscle. This muscular attachment as well as its position relative to the shoulder girdle fixes its identity as the homologue of

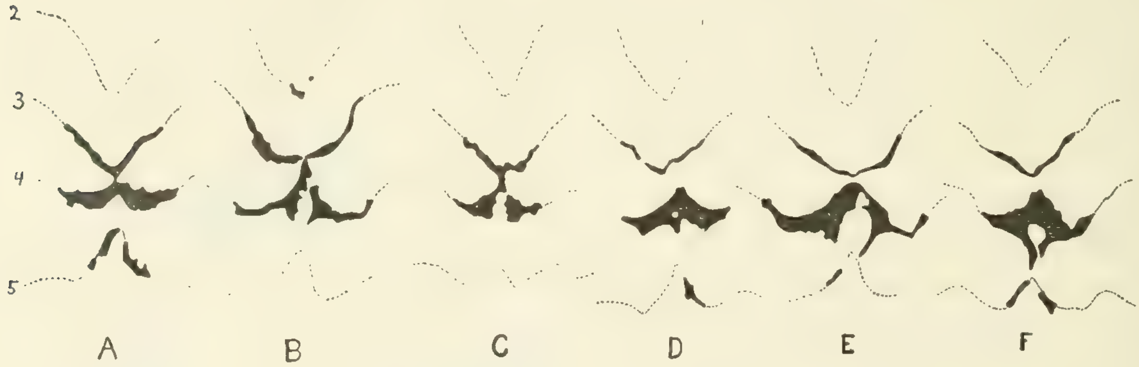


Fig. 6. Sternal pieces of six different individuals, showing variation.

the rhomboidal sternal plate of the higher Urodela, and it would seem probable that this latter has resulted from the development of this piece alone. The sternebrum associated with the 3d myocomma forms a long and slender open V, which may or may not be continuous with the sternebrum of the 4th. Sternal elements are often found both in the 2d and in the 5th myocomma, usually as a pair of cartilages, or as a unilateral piece. Of these, the one associated with the 5th myocomma is much the more frequent, being found in rather more than half of the specimens thus far examined, either upon one side or both. Sternal elements in the 2d myocomma are rarely seen.

Ribs.

These have already been partly described with the transverse processes of the vertebrae. In the larva they are cartilaginous and are directly continuous with the two cartilaginous rods enclosed in the osseous transverse process, and are thus bifurcated at their proximal end. During the later process of ossification the ribs become ossified as separate pieces and the cartilage remaining between the proximal ends of the ribs and the sheaths of the vertebral rods becomes divided across, thus furnishing two sets of articular cartilages. By the shape of the first two ribs in the adult, it would seem that both of the rods are equally involved and simply fuse to form the ribs, but farther down the ventral or capitular attachment retains its full size and importance, while the dorsal one, although more in the same line with the free end, becomes much reduced, and in many vertebrae its attachment is merely ligamentous. Thus, described anatomically, the ribs of the 2d and the 3d vertebrae possess almost equal capitular and tubercular heads, and show a tendency to become bifurcated at their tips. In the ribs of vertebra 4 to 6 the two heads are still almost equal but the distal part of the rib is a simple rod; and farther down, from about the 8th vertebra on, the capitular head forms the main attachment, and meets at a decided angle the straight piece formed by the free end and the tubercular head. The sacral rib possesses two very large and equal heads, but is not bifurcated distally, and beyond the sacrum the rib element is a variable quantity (*v. sup.*). It would thus seem, judging from purely anatomical evidence, that the condition described by Göppert as characteristic of Necturus is not a universal one applicable to

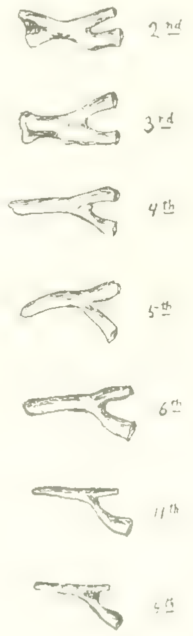


Fig. 7. Ribs taken from the right side of the body and placed so as to show the anterior aspect. The tubercular head is above and the capitular below. The numbers refer to the vertebra to which each rib belongs. × 2.

all of the vertebrae, but is restricted to a certain region, approximately that of vertebra 8 to 18.

It would seem important to investigate the development of transverse process and rib in certain of the other vertebrae, for example the 2d and the 4th. Regarding the sacral vertebra and its rib, as stated previously, Göppert's conclusion, which does not allow a complete homology with the rest of the vertebral column, seems anatomically improbable.

THE SKULL AND VISCERAL SKELETON.

Anatomically, the bones of the head consist of (1) the skull in the restricted sense, which includes the cranium, the ear capsules, and the upper jaw pieces, (2) the nasal and optic capsules, and (3) the visceral skeleton, represented by the mandible, the hyobranchial apparatus, and the laryngeal cartilages. In point of origin the elements are three in number: (1) the primitive cartilage, still seen in the sense capsules, the primordial cranium, and the most of the visceral skeleton; (2) cartilage bones, or ossifications of localized portions of the primary cartilage; and (3) dermal bones of integmental origin, investing the surface of the cartilage in skull and mandible.

Although there are osseous elements from two sources, the proportion of unossified cartilage left in the adult head is very great and compares in this respect with the condition seen in the Chondrostei rather than with that of other fishes or of most amphibians. This large amount of cartilage is very suggestive of an embryonic or immature form, and suggests either the possibility which has already been frequently expressed, that Necturus is in a sense a permanent larva, as is the case with the Axolotl, or that it is an exceedingly primitive form, perhaps nearer the fishes than any other amphibian.

An orderly treatment of this complex bit of anatomy is extremely difficult and may perhaps be facilitated by the presentation of a classification of the subject, which will be adhered to in the later description.

GENERAL DESCRIPTION.
THE CHONDROCRANIUM.
THE OSSEOUS ELEMENTS.
  (a.) Otic and occipital regions.
    1. Pro-otic.
    2. Opisthotic.
    3. Exoccipital.
    4. Quadratum.
    5 and 6. Paraquadratum and operculum.

- (b.) Brain case.
  - 1. Frontal.
  - 2. Parietal.
  - 3. Parabasal.
- (c.) Upper jaw.
  - 1. Maxillary arch.
    - a. Premaxillary.
  - 2. Palatopterygoid arch.
    - a. Vomer.
    - b. Palatopterygoid.

THE VISCERAL SKELETON.
- (a.) General morphology of the arches.
- (b.) Mandible.
  - 1. Dentale.
  - 2. Angulare.
  - 3. Spleniale.
- (c.) Hyobranchial apparatus.
- (d.) Suspensorial relations of the hyoid.

THE FREE SENSE CAPSULES.
- (a.) Nasal capsule.
- (b.) Optic capsule.

THE TEETH.

COMPARISON OF NOMENCLATURE.

General Description of the Skull and its Parts.

The term "skull" is used here in its most restricted sense and does not include either the mandible, the hyobranchial apparatus or the nasal and optic capsules. These elements are for the most part easily detachable from the firmly consolidated skull, and are thus, in the anatomical sense, not to be included with it. A single exception may be made in the case of the nasal capsule with regard to which the usage of authors differs, since, although anatomically distinct in Necturus, it belongs genetically to the primordial skull. Wiedersheim, for example, who is correct from the morphological standpoint, figures it in his drawing of the skull, while both W. K. Parker (in Proteus) and Huxley fail even to find it. In this paper it will be omitted from consideration at present to receive special treatment later on.

The skull, then, denuded of all its extraneous elements, will present an appearance much as is given in figures 2 and 3 (plate 63). The general outline suggested a pentagon to Huxley, but in order to see it as such, one should imagine the ligaments restored that stretch from the outer end of the premaxillaries to the quadrates. The five angles of the pentagon may be named from the bones that compose them, (1) premaxillary, (2 and 3) two quadrate, and (4 and 5) two opisthotic; and the five sides in a similar way may be termed (1) occipital, (2 and 3) the paraquadrate, and (4 and 5) the palato-pterygoid. When dissected or macerated sufficiently to show its parts, it gives the distinct and correct impression of a cartilaginous structure overlaid by flat dermal bones laid on and overlapping "like shingles," to borrow Parker's apt comparison, and showing in places certain intervals through which the primordial skull and its ossifications are distinctly seen. When viewed dorsally (pl. 63, fig. 2) the most conspicuous dermal elements are the frontals and the parietals, which form almost the entire roof, and at the anterior end of the former appear the little premaxillaries. Of the maxillary arch, which normally extends from the outer end of the premaxillary to the quadrate, there is no trace, other than a firm ligament when in the recent state, but the inner arch, parallel to this, is well represented by the vomer and the palato-pterygoid, the outer edges of which are seen in the figure. The only other dermal bones visible from above are the paraquadrates which are seen extending along the postero-lateral sides of the pentagon. The dorsal aspect displays also parts of four cartilage bones: the quadrates forming the antero-lateral angles, the pro-otics and opisthotics in the interval between the parietals and paraquadrates, and the exoccipitals which border the foramen magnum and form the condyles. Upon the ventral side (pl. 63, fig. 3) the most conspicuous bone is the huge parabasal, a dermal bone nearly covering the roof of the mouth, anterior and lateral to which are seen the dentigerous premaxillaries, vomers, and palato-pterygoids. The paraquadrates form a part of the outer margin and a conspicuous process from them is attached to a similar process that projects from a very small oval bone, the operculum, which closes the opening into the otic capsule. The same four cartilage bones seen from the dorsal side appear here, three of which strengthen the otic region while the fourth forms the suspensorium for the attachment of the mandible.

The Chondrocranium.

If, now, as may be easily accomplished in a macerated skull, the dermal or "shingle" bones be carefully removed, there remains a very curious piece of cartilage suggestive of an inner framework, the primordial skull, or chondrocranium. The cartilage bones, previously noticed and now entirely uncovered, are very evidently the result of localized processes of ossification within this, which have taken place in what was once a continuous cartilaginous mass, the homologue of the wholly cartilaginous skull of the present Selachians.

The chondrocranium consists essentially of a delicate framework which runs around the entire cranial cavity and with which certain other cartilaginous elements are associated in varying degrees of intimacy of relation. The framework consists in the embryo of a pair of lateral bars, placed parallel to one another and divisible into an anterior element, the trabecula, and a posterior, or parachordal element. In the adult these names are retained as designations for the regions corresponding to those elements, the trabecular region being that anterior to the otic capsules, while the part associated directly with the capsules themselves is the parachordal region. Posteriorly, between the otic capsules the frame is completed by a pair of cartilaginous bands or arches, of which one, the supra-occipital arch,[1] passes dorsal to the nerve cord, and the other, the basi-occipital arch, lies ventral to this latter part. According to Miss Platt, the supra-occipital arch is really the neural arch of a vertebra anterior to the atlas, which has fused with the skull to increase its strength. At the anterior end of the skull the frame is completed by the development of an internasal plate which connects the convergent trabeculae. Anterior to this the free ends of the trabeculae are continued a short distance in the form of small rostral processes.

Of the originally external elements, the two large otic capsules are the most intimately related and are completely fused with the posterior portion of the primary part and thus form the largest and most voluminous portion of the chondrocranium. Anterior to these are the semi-detached quadrate cartilages, connected with the sides of the trabecular frame by a narrow process, the trabeculo-quadrate isthmus. Still farther forward and separated from the latter by an interval in which are situated the eye and its accessory organs, appears a pair of distinct cartilages, attached to the trabeculae by connective tissue. These are the ante-orbital processes plainly representing a rudiment of the subocular arch, or pterygo-quadrate process, so enormously developed in the frog and other Anura, an homology suggested by W. K. Parker's term of "ethmo-palatine process."

The other cartilaginous parts topographically associated with the chondrocranium are the nasal and optic capsules, of which the former lies directly upon the anterior end of the completed skull, and barely comes in contact with the chondrocranium, while the latter is completely isolated. These parts will receive separate treatment later.

The ossifications of the chondrocranium (= "cartilage bones") are few in number in comparison with those of most Urodeles and consist of but four pairs: (1) the quadrates, used to form a strong support for the mandible, (2) the exoccipitals, forming the condyles and thus strengthening the important articulation of the head with the vertebral column, and (3 and 4) two ossifications of the otic capsule. These, of which the anterior is the pro-otic, and the posterior the epi- and opisthotic combined, are in the form of hollow cups which fit over the anterior and posterior ends of the otic capsule, looking, to borrow W. K. Parker's vivid simile (in Proteus), "as if they were ready to dehisce transversely like the pyxidium of the pimpernel (Anagallis)."

---

[1] Miss Platt objects to the term "occipitale superius" for the dorsal cartilaginous arch on the ground that the supra-occipital is not an amphibian bone and prefers "interoccipitale," as suggested to her by Gaupp. This term, however, leaves out of account the ventral arch, unless we use the terms "interoccipitale dorsale" and "interoccipitale ventrale" which are cumbersome and possess the disadvantage of the substitution of new terms for old and readily understood ones. Moreover, a portion of the Amniote supra-occipital is preformed in cartilage, and it seems more than probable that there is at least a partial homology between it and the cartilaginous arch found here. The same may also be said of the basi-occipital piece.

The Osseous Elements.

The otic and occipital regions.— 1. PRO-OTIC. This very irregular bone consists essentially of a conical cap to which are added four projecting processes, one upon the inner and three upon the outer aspect. The inner process, the ala, is flat and wing-like and is applied along the outer edge of the base of the trabecula. Of the three processes which project from the external face of the bone, the two anterior ones, dorsal and ventral quadrate processes, possess concave and roughened articular surfaces to receive corresponding processes of the quadrate cartilage. The ventral process may be considered an extension of the ala, and it receives a rounded protuberance situated in the middle of the posterior margin of the cartilaginous quadrate. The dorsal quadrate process forms the external dorsal edge of the bone and displays a more elongated articular surface for the reception of the otic process of the quadrate. The remaining external process has no relation with other skeletal parts and its probable use is that of attachment for some important muscle or ligament, as it is very constant in appearance and always well

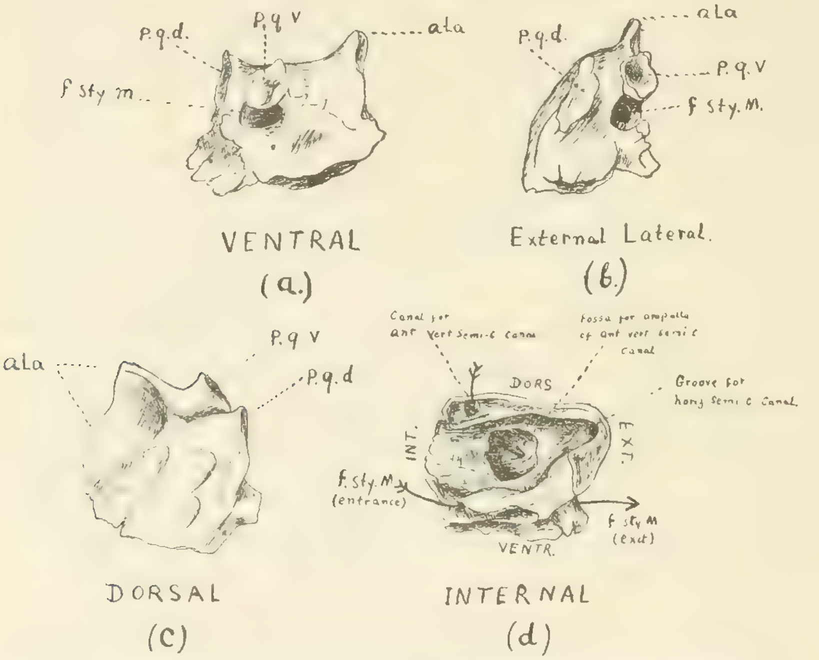


Fig. 8. Four views of the right pro-otic. p. q. d., dorsal quadrate process; p. q. v., ventral quadrate process; f. sty. m., stylo-mastoid foramen.

developed, but this point must be left for later investigation. It runs parallel to and very near the ventral quadrate process, and between the two there is thus formed a deep notch, at the bottom of which is seen the outer opening of the stylo-mastoid canal, that transmits the facialis nerve. This canal enters the pro-otic at its inner posterior margin, traverses almost its entire ventral wall and emerges by the notch just described.

Internally the pro-otic is hollowed out for the reception of the anterior portion of the membranous labyrinth. At the junction of its internal and dorsal edges there is a canal for the transmission of the anterior vertical semi-circular canal, the ampulla of which lies in a deep but narrow excavation at the apex of the cone. The anterior portion of the horizontal semi-circular canal is lodged in a groove upon the outer side of the internal excavation, just beneath the dorsal quadrate process.

The pro-otic may come in contact with three bones, the actual condition varying with the age and degree of development. Its ventral surface is always overlapped by the parabasal, and is usually somewhat roughened over the region of contact. The parietal partly overlaps it dorsally. In large and mature specimens the anterior border of the operculum may touch it upon the ventral side.

2. OPISTHOTIC. This bone consists of a hollow cup, forming the posterior lateral angle of the skull, and investing the posterior part of the otic capsule. It is irregularly conical in shape, being somewhat flattened like a triangular pyramid, and thus presents externally for examination three nearly flat surfaces, a dorsal, a ventral, and an internal lateral, facing the occipital condyle. Of these surfaces, the dorsal is the flattest, the ventral is quite convex, and the internal lateral is marked by a deep groove along which lies the vagus group of cranial nerves. The apex of the cone or pyramid is directed backwards and a little outwards, and terminates in a slightly elevated process, which may be called the mastoid for convenience, since it has some analogy with the mammalian process of that name.

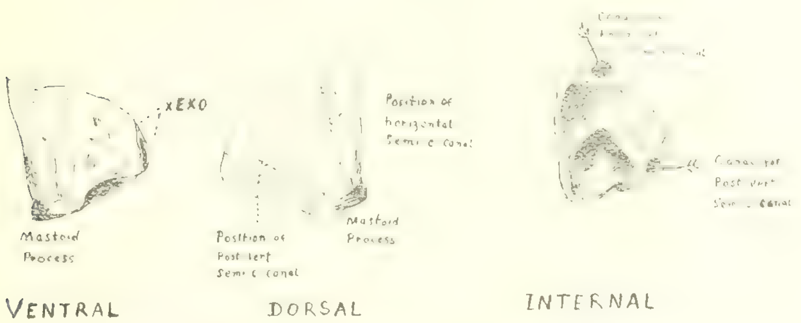

xEXO
Mastoid Process
Position of Post vert Semi c Canal
Position of horizontal Semi c Canal
Mastoid Process
Canal for Post vert Semi c Canal
VENTRAL
DORSAL
INTERNAL

Fig. 9. Three views of the right opisthotic. × 3. Taken from a specimen smaller than in the case above.

Internally the bone presents two canals, a large central depression, and in the bottom of the latter a still deeper recess into which the canals open. The two bony canals, which are excavated in the dorsal wall of the hollow cone, may be distinguished as the lateral and median, and lodge, respectively, the horizontal and posterior vertical semi-circular canals of the membranous labyrinth. The ampullae of these two canals lie at their posterior union and are situated in the deep recess. The large central depression forms a portion of the median chamber which contains the membranous vestibule with its large otolith. The opisthotic comes in contact with two bones, the paraquadrate and the exoccipital. The former merely overlaps with its posterior portion the outer margin of the opisthotic, but the exoccipital forms, at least in large specimens, a definite union through the medium of distinct processes projecting from the two bones.

The side to which a given opisthotic bone belongs is best determined by the canals and the deepest recess. The canals lie nearest to the dorsal surface and the recess is on the internal side.

3. EXOCCIPITAL. This pair of bones, the bodies of which form the occipital condyles, embraces and defines the foramen magnum and, with the addition of dorsal and ventral cartilaginous arches, entirely encloses it. Each bone consists of a body and two flat processes, the supra- and basi-occipital alae. The body is practically identical with the condyle, and its posterior aspect forms a rounded surface for articulation with the atlas. The dorsal or supra-occipital ala is nearly perpendicular to the rest of the bone and to the floor of the skull and is set obliquely, at an angle of about 45° with both longitudinal and transverse axes of the head, so that, when viewed from above, the median occipital region forms a conspicuous re-entrant angle. This ala arises from the body as a narrow stalk which rapidly widens, and thus resembles a triangle resting upon its apex. The dorsal margin, or base of the triangle, is grooved for the reception of the cartilaginous arcus supra-occipitalis which spans the median interval between this ala and its opposite.

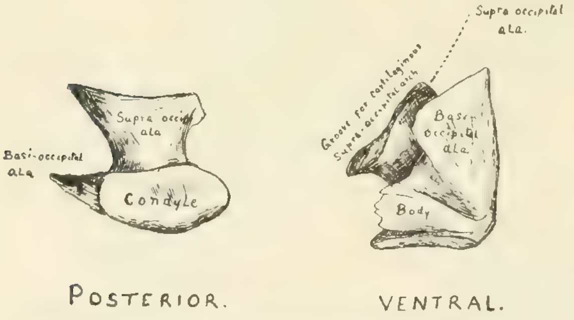


Fig. 10. Two views of the right exoccipital. × 3.

The ventral or basi-occipital ala lies exactly in the horizontal plane, coincident with that of the parabasale, and is applied so closely to this latter bone by its ventral surface that the separation is often attended with some little difficulty. Both W. K. Parker and Wiedersheim found the exoccipitals in Proteus actually a part of the parabasal, or, as the latter expresses it, "synostotisch verbunden." This is nearly the case in Necturus, but, as the two bones are really separable in all cases tried, it is possible that this may be the actual condition in Proteus also. The ventral ala is triangular in shape but is attached to the body of the bone by a side and not an angle, and, when viewed from the ventral side, forms with the condyle a right-angled triangle, the right angle facing the middle line and the hypothenuse forming the lateral side. The small interval formed between the opposing right angles of the two exoccipitals is spanned by a ventral cartilaginous arch, the arcus basi-occipitalis, which, with the supra-occipital arch and the two bones under consideration, completes the enclosure of the foramen magnum.

This basi-occipital cartilage is of greater extent in young and larval animals, and the ventral alae result from the gradually increasing ossification of its lateral ends. As this process continues towards the center, the inner angles of the bone nearly touch one another in old adults, while the cartilaginous arch is correspondingly diminished.

The exoccipital comes into contact with four bones: (1) the parabasale, which is closely applied to the basi-occipital ala, (2) the opisthotic, which, in adults, touches both the body and the dorsal margin of the supra-occipital ala, (3) the parietal, a bit of the posterior margin of which becomes applied to a corresponding portion of the dorsal margin of the supra-occipital ala, within its contact with the opisthotic, and (4) the atlas, which articulates with the condyles by a movable joint.

The natural relations of an isolated exoccipital are best learned from the flat ventral surface. The condyle is posterior and the long straight edge is internal.

4. QUADRATUM. This is primarily a cartilaginous element, associated with the primordial skull, and representing the proximal (posterior) end of the palato-pterygoquadrate arch, the functional upper jaw of the Selachians. In the Anura this arch is entire, but in Necturus it is represented by its two ends alone: the antorbital process, which represents its anterior, and the quadratum, its posterior portion.

Functionally it serves as a "suspensorium," or piece interposed between the skull and the mandible, and forming an articular surface for the latter. This joint occurs at its outer anterior angle, and that region of the quadrate becomes ossified, plainly to give strength to this very important joint. It thus happens that there is in the adult, both an osseous and a cartilaginous quadrate, the former being situated externally and the latter towards the median line.

The irregular shape of the quadrate taken as a whole may best be seen by a reference to figures 10 and 11 (plate 64). The external osseous portion consists of an anterior articular process of very hard bone, fitted with an articular socket to receive the rounded cartilaginous knob (articulare) of the mandible, and a hollow trough-like posterior process fitted over the outer edge of the cartilage much as in the case of many of the dermal bones. The cartilaginous portion consists of a flattened plate which attaches by its broadest side to the bony portion and tapers down to a narrow isthmus as it approaches the skull. Contact with the latter is formed by means of anterior and posterior extensions of the isthmus, which become applied to the outer side of the trabecula just in front of the otic capsule. It is difficult to determine, in a piece of this shape, the location of the processes cited by authors in their description of the quadrate of other Amphibia. The posterior lateral extension which runs along the side of the bone is probably the otic process, and the narrowed part, or its posterior prolongation, the pedicel. Of the two processes which form the isthmus and become applied to the trabecula, the anterior one may possibly be the ascending process. A slight angle seen in the anterior margin is doubtless the rudiment of the "cartilaginous pterygoid" found in most Urodeles, the extension of which to the antorbital process would form the palato-pterygoid arch which is wanting here. Aside from its attachment to the trabecula, the quadrate, osseous and cartilaginous, enters into more or less complete attachment to four bones. As described above, two processes of the pro-otic form quite definite articulations with the quadrate cartilage, the ventral one receiving an articular surface formed by a thickened piece of cartilage in the middle of the posterior margin, and the dorsal one being applied along the inner edge of the otic process. The paraquadrate overlaps it externally, and the outer posterior corner of the palato-pterygoid fits into a groove in the inner side of the articular process and overlaps a raised area of the quadrate cartilage. The cartilaginous articulare of the mandible forms a movable articulation with it.

In determining the position of an isolated osseous quadrate it may be remembered that the side showing the hollow groove is internal, that the larger end is anterior, and that the broader, plainer surface is dorsal.

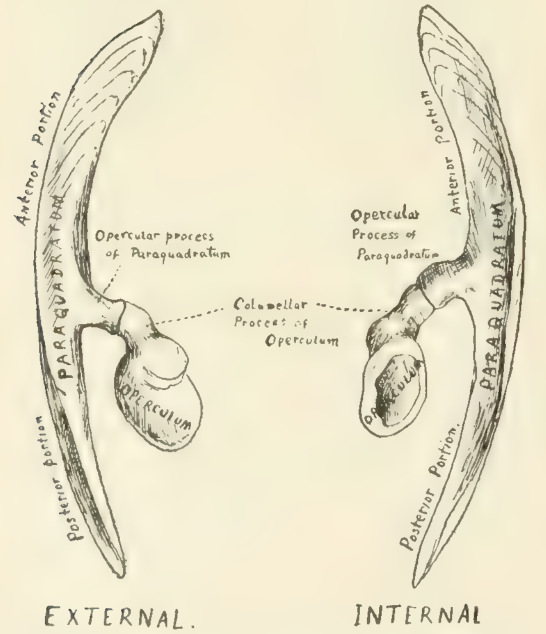


Fig. 11. Right paraquadratum and operculum. Two views. × 3.

5 and 6. PARAQUADRATUM AND OPERCULUM. These elements, of which the first is a dermal bone, and the second an ossification of a detached portion of the otic capsule, are closely connected topographically and joined to one another by a strong ligament which unites processes in each bone mutually directed toward the other. The paraquadratum, the shape of which suggested a boomerang to Huxley, attached in its normal manner to the little discoidal operculum, presents the appearance given in figure 11. When in place upon the skull, the paraquadrate lies along the outer side of the otic region, forming the two sides of the pentagonal outline of the skull designated above as "paraquad-

rate," while the operculum fits tightly and exactly into the fenestra ovalis, a large lateral opening in the cartilaginous otic capsule.

The most conspicuous character of the paraquadrate is the short and blunt opercular process, which projects from the inner edge of the curved bone at approximately the middle and thus divides it into two nearly equal portions, the anterior or quadrate, and the posterior, or opisthotic halves. These two halves are nearly flat, or like very shallow troughs, the planes of which are set nearly at right angles to one another; and when in place, the anterior portion is placed nearly perpendicularly to the skull overlapping the quadratum along the side, while the posterior portion is nearly horizontal and covers the outer part of the dorsal surface of the opisthotic.

The paraquadrate is always connected with three bones and may possibly come in contact with two more. By its opercular process it forms a definite articulation with the columellar process of the operculum, and its two flat portions are applied to the outer surface of the quadrate and opisthotic. Aside from these, its anterior and posterior ends may touch the outer corners of the palato-pterygoid and parietal respectively. If an isolated paraquadrate be held so that the opercular process is directed downwards, it is in its normal position and the position of the planes of the anterior and posterior portions will serve to locate it.

The operculum fits something like a stove lid into the fenestra ovalis, an oval opening in the cartilaginous otic capsule. It consists of a flattened oval base or body bearing upon its outer surface an irregular columellar process. By means of this process it articulates with the opercular process of the paraquadrate and normally touches no other bone, although in old animals the pro-otic bone may enlarge sufficiently to come in contact with its anterior edge. The columellar process is directed upwards and a little forwards, and will thus give the proper orientation for the bone.

The homologies and, consequently, the nomenclature of these two bones have been a matter of much uncertainty and varient treatment among authors. For the first of these I have selected the term "paraquadratum" on the authority of Gaupp, who has proposed it as at least a provisional term to indicate the dermal encasing piece associated in the amphibians with the quadrate. He apparently inclines to the belief that this element may prove homologous with the mammalian tympanicum, a term by which he designates the piece in his revision of the "Anatomie des Frosches." The operculum has become so universally identified with the stapes of higher forms that in the first writing of the manuscript for this work the word "stapes" was used and its probable homology stated. I was led to a change of this view by the examination of a set of slides of a larval Necturus of 44 mm. in which the part in question arises as a semi-detached bit of the cartilaginous otic capsule, precisely as was seen by Stöhr in Triton and Siredon. This was equally evident and presented a similar appearance in a series taken from a larva of 26 mm. This observation, which seems perfectly clear and unassailable, and which corroborates the results given by Stöhr in other Urodeles, is absolutely at variance with the statement of Miss Platt, who says that "it arises independently" and identifies as its anlage a mass of cells which, in an embryo of 19 mm., is situated just in front (outside) of the fenestra ovalis, and between it and the end of the ceratohyal. It is possible that this anlage may represent a true columella or hyomandibular cartilage, which may later become fused with the true operculum to form its projecting external process, although in the larvae of 26 mm. and 44 mm., the series which I have examined, I can find no trace of such a double origin of the parts in question.

The brain case.—This is formed in great part by five dermal bones, the two frontals, two parietals, and the parabasale, of which the first four form its dorsal, lateral, and anterior walls, and the parabasale its floor. The box formed by these is deficient posteriorly, where it is completed by the otic capsules and other cartilaginous elements with their ossified areas. Above, each frontal is so completely welded to its accompanying parietal by means of interlocking splints that they practically form one bone while the two sets of united pairs meet in the median line by means of somewhat thickened flat edges, forming symphyses. Upon the ventral surface of this roof, both bones send down extensive processes that lie just within the trabecular arch of the primordial skull and make an extensive ridge in the form of a long narrow U, the loop being directed anteriorly. This ridge forms the front and sides of the brain case and at its ventral edge is everywhere in contact with the parabasale.

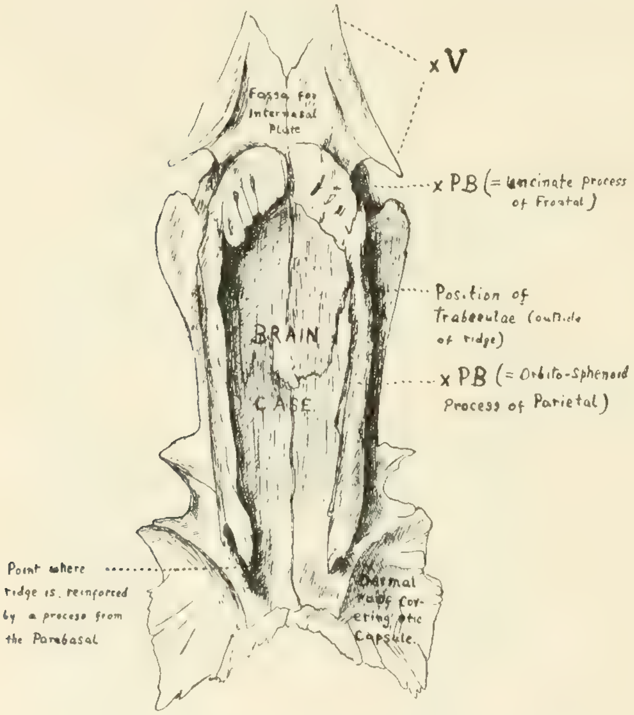

x V
Fossa for Internasal Plate
x PB (= Uncinate process of Frontal)
Position of Trabeculae (outside of ridge)
BRAIN CASE
x PB (= Orbito-Sphenoid Process of Parietal)
Point where ridge is reinforced by a process from the Parabasal
Dermal roof covering otic Capsule.

Fig. 12. The roof of the brain case seen from beneath. × 3. This is composed of the two frontals and the two parietals, upon the ventral side of which is developed a series of processes which together form a U-shaped ridge that forms a front and sides to the case. Contact surfaces for other bones are designated by an x and the abbreviations of the bone involved.

The result of this singular formation is that in Necturus the lateral walls of the brain case are formed of solid dermal bone reinforced externally by cartilage while in most Urodeles the walls are formed by the cartilaginous trabeculae or in part by an ossification in these elements, the orbito-sphenoid. A foramen for the olfactory nerve is formed at the junction of the frontal and parietal contributions to this ridge; other nerves, as the trigeminus and facialis, emerge from the cranial cavity just posterior to it, but the nerves to the eye muscles and the opticus pass through tiny foramina, running very obliquely through the process itself.

The floor of the brain case is formed by the very extensive parabasal, which receives upon its dorsal surface the lateral processes projecting from the roof, and reinforces them posteriorly by a low ridge topographically continuous with them. The details of the separate bones are as follows:—

1. FRONTAL. The frontals form a little more than a third of the dorsal surface of the skull. They lie in contact with one another for about two thirds of their length, diverging anteriorly to form a pair of short premaxillary processes, and posteriorly to form the longer and thinner parietal processes. A single frontal, isolated from its surroundings, resembles a flat and quite irregular splinter of bone from the under (ventral) side of which hangs a partially detached plate directed backwards, the processus uncinatus of Wiedersheim, which forms the anterior portion of the U-shaped ridge described above. The notch enclosed between this process and the main body of the bone transmits the olfactory nerve and is converted into a foramen by the addition of the antero-lateral process of the parietal and the trabecula. A conspicuous process upon the outer margin of the bone in this region, directed backwards, and seeming to belong to the uncinate process rather than to the main body of the frontal, assists also in the formation of the olfactory foramen and may be termed the olfactory process.

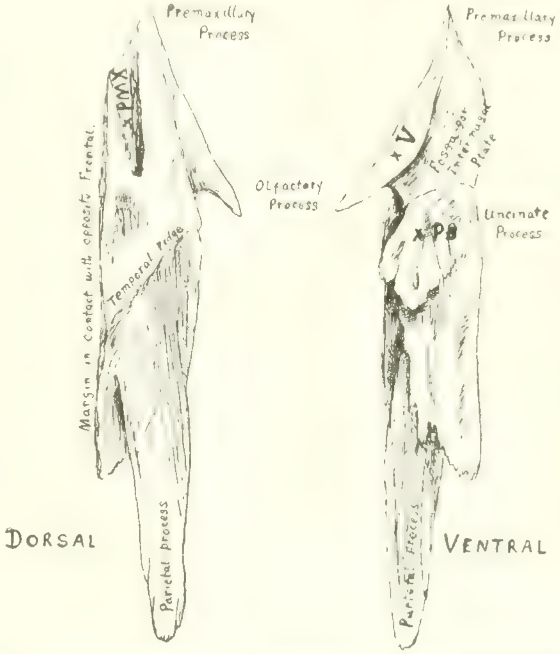


Fig. 13. Two views of right frontal. × 3. Contact surfaces with other bones are designated by an x.

Upon the ventral side of the bone are seen two roughened ridges for the attachment of other bones. Of these the more anterior is a curved ridge connecting the olfactory and premaxillary processes and serving for the attachment of the vomer; the other involves the ventral surface of the uncinate process and comes in contact with the parabasal.

Between them is a flattened depression, the internasal fossa, which lodges the internasal plate of the chondrocranium. The dorsal side possesses few features of interest. At the anterior end is a longitudinal groove in which rests the ascending process of the premaxillary and farther back is an oblique temporal ridge, extending from the olfactory notch to the middle of the interfrontal suture, and serving as the anterior limit of the temporalis muscle.

2. PARIETAL. This is the most irregular bone of the skull, and the largest, with the exception of the parabasal. It possesses extensions in several directions, but it is so irregular that the number of definite processes, of which Wiedersheim enumerates five, is somewhat arbitrary. Of these, the most important functionally as well as anatomically, is the longitudinal ridge upon the ventral side, the edge of which comes in contact with the parabasal, and which functionally replaces an orbito-sphenoid and serves as the side of the brain case. This may be called the orbito-sphenoid process, as suggestive of its function, and this process together with the uncinate process on the frontals completes the U-shaped ridge mentioned above. This ridge is perforated by several very slanting foramina for the transmission of the nerves of the eye muscles, but the exact identification of these must be left for later investigation. The irregularly curved and very thin dorsal surface may be conveniently divided into a nearly flat anterior portion and a decidedly convex posterior portion, taking its shape from the otic capsule which it covers. From the anterior portion proceed three processes, an antero-median, an antero-lateral, and a quad-

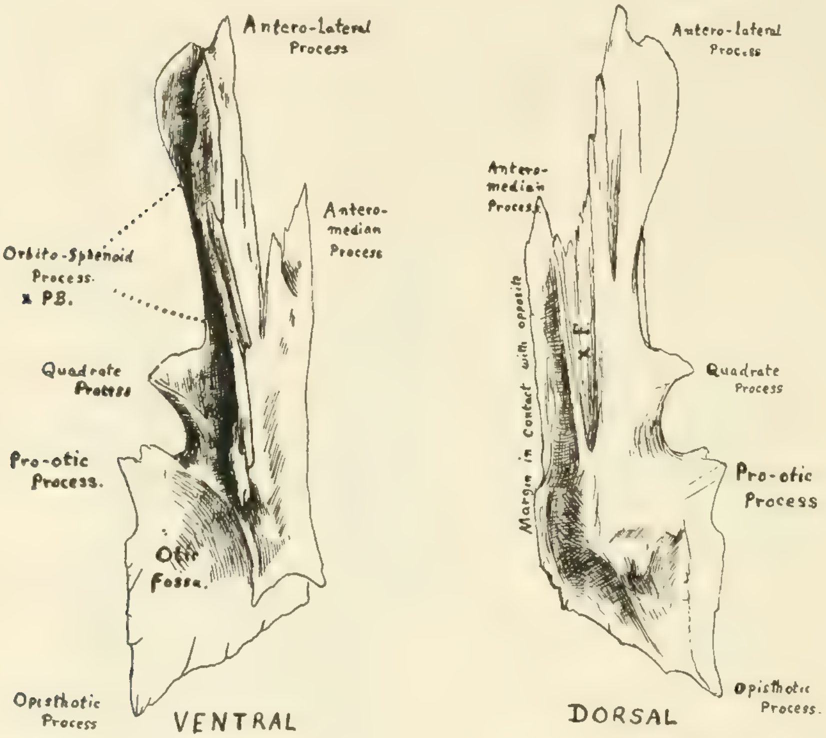


Fig. 14. Two views of right parietal. × 3. Contact surfaces with other bones are designated by an x.

rate. The first two receive between them the parietal process of the frontal, and the antero-lateral one, which is much the larger, reaches the olfactory region and assists in the formation of the olfactory foramen. This process bears upon its ventral side a large portion of the orbito-sphenoid process. The quadrate process is small and flat, and projects over that part of the quadrate cartilage designated above as the "isthmus." The outline of the posterior portion is practically a square, of which the two outer corners are obvious, the posterior one being considerably prolonged. These may be termed respectively the pro-otic and opisthotic processes in reference to the bones which they partially overlap. This portion forms a thin outer covering for the otic capsule and corresponds to it in shape, being convex above and concave beneath. It forms the otic fossa of the ventral surface.

There are several prominent muscular ridges upon the dorsal surface of the parietal, the most important of which are several irregular ones upon the posterior portion and a median one formed between the two bones and prolonged into a median intermuscular septum.

3. PARABASAL. This is the flattest and most extensive bone of the skull and forms nearly the whole of the floor of the brain case, and at the same time the roof of the mouth. It is nearly in the shape of a parallelogram with rounded corners, but is a little broader in the otic region and becomes somewhat narrowed anteriorly. It is almost without special features other than the impressions made by the bones which come in contact with it, the frontals and parietals upon its dorsal, and the vomers upon its ventral surface. Upon the dorsal surface at the posterior end there is a pair of low lateral ridges which reinforce the orbito-sphenoid processes of the parietal and

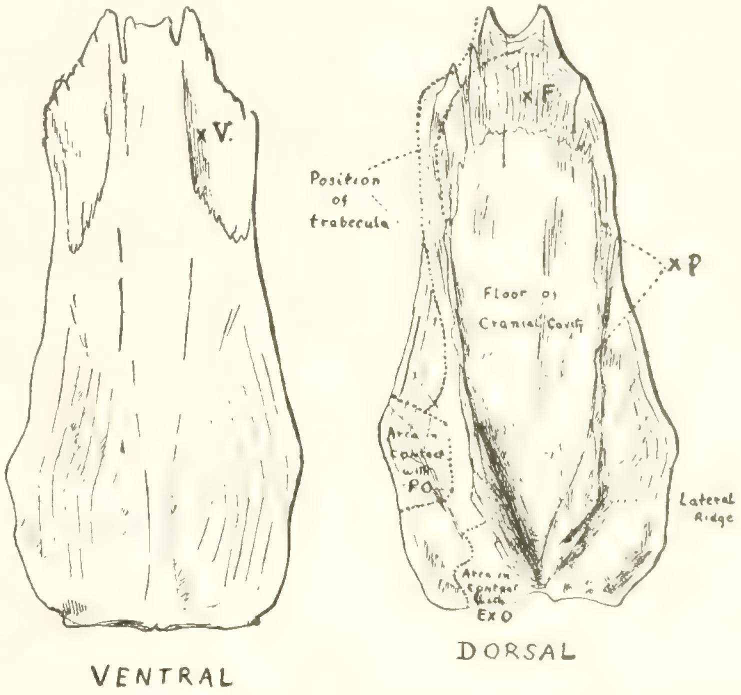


Fig. 15. Two views of the parabasal taken from different individuals. The view of the dorsal side is 4 times enlarged, that of the ventral, being from a much larger individual, but 2½. Contact surfaces with other bones are designated by an x.

converge at the posterior end. There is necessarily a slight depression between them, but anything as marked as the depression described by Wiedersheim and likened to a "sella turcica," I have failed to find. Probably this outline would be much more noticeable in cross sections, which were studied extensively by this author, and in a young animal it is likely that it would be proportionally more marked. The parabasal normally comes into contact with ten bones, eight upon the dorsal surface and two upon the ventral. Dorsally there are found in order, the two frontals, and the two parietals, by their uncinate and orbito-sphenoid processes respectively; the two pro-otics, and the two exoccipitals, the latter almost anchylosed with it in old adults. Upon the ventral side are the two vomers. The palato-pterygoids and the opisthotics come very near the parabasal, but form no definite area of contact.

The upper jaw.— Under this term may be included all the dentigerous bones of the skull proper, as the teeth of all these oppose those upon the mandible. In this group both of the typical arches are represented, the maxillary and the palato-quadrate, or the "inner" and "outer arches" of W. K. Parker, the former by the premaxillaries and the latter by the vomers and palato-pterygoids. Each of these arches bears a row of teeth, and, when the mouth is closed, the single row on the mandible is received between the two upper rows. The internal or palatine row is longer than the external or maxillary.

1. THE MAXILLARY ARCH. This arch is represented in most Urodeles by both premaxillaries and maxillaries, the latter extensive and ending in long, backward projecting processes which, in the recent state, are attached by strong ligaments to the quadrates, thus making the arch a complete one. In Necturus it suffers much reduction and is represented by the premaxillaries alone. The maxillary fails completely, and no rudiment of it seems to be present at any developmental stage. Hyrtl describes a dried specimen with a small but tooth-bearing maxillary upon one side. Neither Huxley nor Wiedersheim could find a trace of it, and in an examination of more than fifty skulls I have never seen it. The specimen described by Hyrtl must have been either an abnormal case or one of mistaken identity.

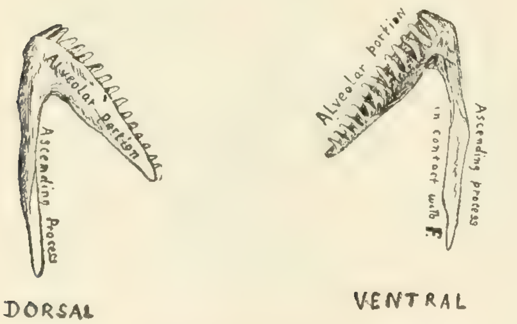


Fig. 16. Two views of right premaxillary. × 3.

a. Premaxillary.— This bone consists of a slightly curved alveolar portion, to the inner end of which an ascending process is added at nearly a right angle. The alveolar portion is placed in an antero-lateral position, ventral to the large nasal capsule, which lies obliquely across it and forms the anterior part of the outer margin of the skull. The ascending process is in the form of a flattened splint and is superposed upon the dorsal surface of the anterior end of the frontal, lying in a shallow groove formed for its reception. This is the only contact between the premaxillary and any of the other bones of the skull; but the extreme tips of the rostral cartilages may touch its ventral surface, and the two premaxillaries almost touch each other at their antero-internal angles.

2. THE PALATO-PTERYGOID ARCH. This arch in Urodeles consists typically of three dermal elements, vomer, palatine, and pterygoid, but owing to fusion or loss of one or more of the elements, it usually appears in a modified form. In some Urodeles the first two of the typical elements fuse and form a broad vomero-palatine, while in others, as is the case in Necturus, the vomer is distinct and the second and third elements fuse to form a palato-pterygoid. Usually in the vicinity of the pterygoid there is a part of the primitive cartilaginous palato-pterygoid arch around which the dermal bones may be supposed to have originated, and this is denominated the "cartilaginous pterygoid." In a few cases (Desmognathus, Batrachoseps) the osseous pterygoid fails, leaving the vomero-palatine as the sole dermal representative of the arch.

a. Vomer.— The main portion of this bone is somewhat triangular in shape and forms the extensive, flattened palatine portion. Added to this upon its outer border appears the alveolar portion, set at right angles to the main part and slightly curved. The palatine portion forms the greater part of the anterior third of the roof of the mouth but the two bones do not meet in the middle line. The inner borders, forming the longest side of the triangle, are quite near one another anteriorly but diverge posteriorly, and in the space thus left appears the parabasale, which also extends along the dorsal side of the palatine process of the vomer, thus doubling the bony roof of the palate over a large extent of the anterior surface. The parabasal does not, however, extend anteriorly as far as the vomerine teeth, and there is thus left a considerable interval, bounded by the above mentioned teeth, the inner borders of the vomers, and the anterior border of the parabasal, where there is no bony roof. This opening is nearly square, and through it, in the prepared skull, there may be

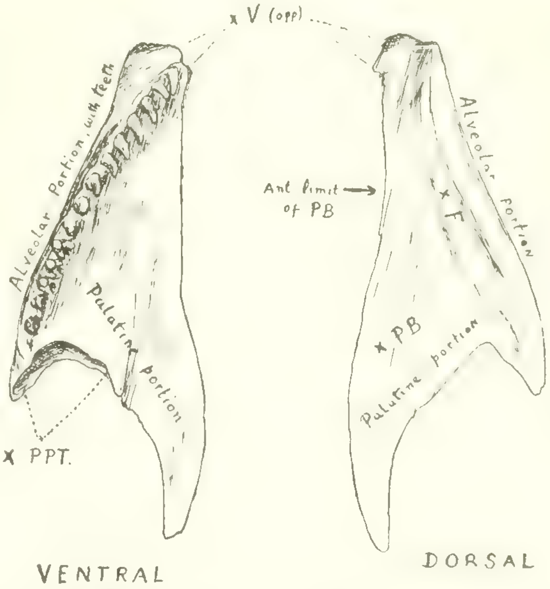


Fig. 17. Two views of right vomer. × 3. Contact surfaces with other bones are designated by an x.

seen the internasal plate of the primordial skull. Viewed from the ventral side, the two vomers may be said to overlap the parabasal, and the areas of contact are clearly marked upon the dorsal surface of the former bone and the ventral surface of the latter. The frontal bone comes in contact with the vomers dorsally, and the articular surface for this forms a long, narrow ridge, running along the lateral border above the row of teeth. At the extreme anterior end, the two vomers come in contact with each other, the symphysis being marked by a few jagged, irregular projections. The postero-lateral border of the palatine portion is recurved and exhibits an articular surface for the anterior end of the palato-pterygoid.

b. Palato-pterygoid. — This is a flattened bone, somewhat in the form of a narrow parallelogram, but with the anterior end rounded. It is set in the skull obliquely to the longitudinal axis and extends from the vomer to the quadrate, articulating with both and with no other bones. Its alveolar portion is small and confined to a short curved ridge upon the outer border at the anterior end. The space between the inner border of this bone and the outer border of the parabasal is in the form of a very narrow triangle and is filled in the recent state by a firm membrane. The orientation of this bone may be easily made by the teeth which are upon the ventral side, at the anterior end, and along the outer margin.

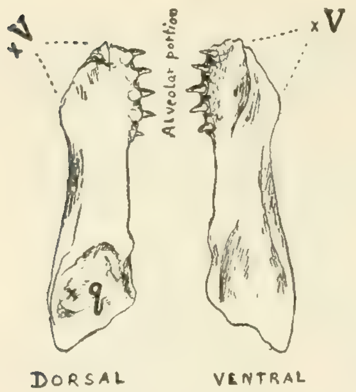


Fig. 18. Two views of right palato-pterygoideum. × 4, (from small specimen). Contact surfaces with other bones are designated by an x.

The Visceral Skeleton.

General morphology of the arches.— The seven visceral arches inherited from the Selachians, and surviving in most higher vertebrates, are represented here, although one of them (the 6th) is vestigial, and appears in the adult as merely an intermuscular septum. Their disposition is as follows: —

1. This arch, forming the functional jaws of the Selachians, possesses typically a dorsal and a ventral segment, of which the former is represented by the cartilaginous palato-quadrate arch, and the latter by Meckel's cartilage of the mandible. Both of these arches, in most higher vertebrates, become encased by dermal bones and lose their identity more or less completely in the adult, the palato-quadrate arch suffering more in this particular than the other. In Necturus the anterior and posterior ends of the palato-quadrate arch survive as the antorbital process and the quadrate cartilage (including its ossification) respectively, and the median portion is unrepresented. The

dermal bones connected with this arch are the vomer and the palato-pterygoid. These as well as the quadrate have been previously described. The ventral segment is represented by a very complete pair of Meckel's cartilages, encased by three dermal bones, the dentale (dentary), spleniale (operculum), and angulare. The proximal, or posterior end of this cartilage forms a rounded articular surface which articulates with the mandibular process of the quadrate, and forms an element often ossified in amphibians, and then known as the articulare.

2. The second visceral arch consists in the Selachians of a dorsal segment, the hyomandibular, and a ventral segment, the true hyoid. The latter piece is always present and well developed in Urodeles, and in Necturus consists of two well developed cartilages upon each side, but opinions differ widely concerning the fate of the hyomandibular. The views which connect it with the stapes of mammals and the columella of reptiles seem to have much support, but any connection between it and the Urodele operculum is evidently disproven by the origin of this latter piece from the side of the otic capsule. It thus seems safe to assert that the dorsal or hyomandibular segment of the second visceral arch has no skeletal representative in Necturus.

3–5. These are the three gill arches which guard and regulate the two gill slits situated between them upon either side of the neck, support the three pairs of integumental branchiae, and furnish attachment for the muscles which regulate them. This association of external branchiae, belonging to the integumental system, with the three gill arches, which in fishes support the internal endodermic gills, has led in the past to a confused suggestion of homology between these genetically distinct structures. The gill arches are represented here by twelve cartilages, five on each side and two in the median line, and all of these pieces are joined with the four of the hyoid arch to form the hyobranchial apparatus.

6. This is the rudiment mentioned above, and represented by an intermuscular septum.

7. This arch is represented by a single pair of cartilages which guard the entrance to the trachea and extend along its sides; the cartilagines laterales, or laryngo-tracheal cartilages.

The parts will now be taken up in detail.

The mandible.—The mandible consists of the four separate elements mentioned above: Meckel's cartilage and the three dermal bones, dentale, spleniale, and angulare. The cartilage is well encased by the dermal pieces, but its surface is exposed along a part of the internal aspect, as well as over a large portion of the proximal, or articular end, where it forms the joint. In the larva the cartilages of the two sides meet at the mid-ventral line, and receive the protection of the dentalia upon their outer side alone, but as these latter bones develop, they expand somewhat at their meeting with one another and form a strong bony symphysis, suppressing the median ends of the cartilage. The dentale is the largest of the dermal bones and covers the entire outer side of the mandible from symphysis to posterior angle. It forms nearly the anterior third of the inner surface, and two thirds of the lower edge, forming, with the lower border of the angulare, the foramen mandibulare. The angulare is next in size and is the main bone of the inner surface, extending along the posterior two thirds of the mandible. It forms the posteriorly directed angular process, and a small part of the bone appears in this region upon the outer surface. The spleniale is very much reduced in Necturus and is in the form of a little oval scale, set somewhat on the inner side, filling an interval between the angulare and the dentale. It is dentigerous and bears a few (5 to 7) teeth, which form a row not exactly continuous with that of the dentale, and opposed to that of the palato-pterygoid in the upper jaw. The details of the above osseous elements follow.

1. DENTALE. This bone gives the contour to the jaw and follows quite closely the general outlines of the head, and thus the posterior part is nearly straight while the anterior third curves somewhat abruptly inwards. It is quite thin and its upper and lower edges are curved inwards, making its outer surface somewhat convex and the inner concave. At the anterior third so much of the lower edge curves in that it forms a fairly broad and flat submental surface involving about half of the total width. The dentale bears a row of teeth which occupy nearly the anterior half. They are inserted along the inner aspect, about half their length appearing above the upper edge of the bone. Just posterior to this row of teeth the upper margin rises a little to form a very rudimentary ramus which receives the insertion of the very stout tendon of the masseter muscle. Internally, the dentale is chiefly characterized by its concavity, which lodges Meckel's cartilage and forms a deep and narrow groove anteriorly which broadens out posteriorly to the full width of the bone.

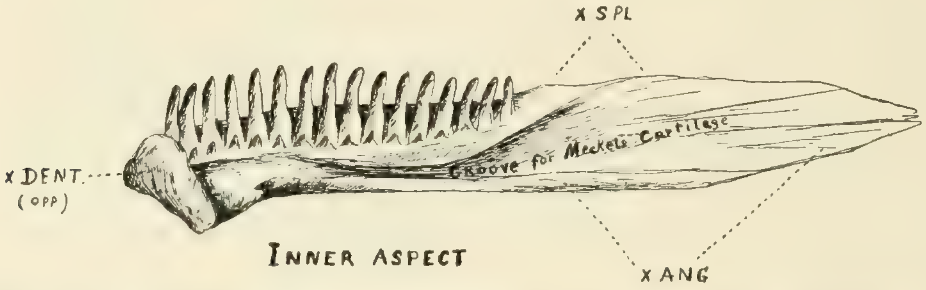


Fig. 19. Internal view of right dentale. × 3. Contact surfaces with other bones are designated by an x.

The two dentalia form a strong symphysial articulation with one another at their anterior ends, a union which, in a macerated skull, often holds long after the separation of the other components of the jaw. The recurved ventral margin of the dentale becomes closely applied upon the inner side of the mandible to the corresponding edge of the angulare and usually completes the formation of the intermandibular foramen. The spleniale comes in contact with it by a portion of its outer surface.

2. ANGULARE. This bone is a curved splint, broad behind and tapering anteriorly into an extremely fine and sharp point. Its outer aspect is concaved to receive Meckel's cartilage, and this surface, together with the inner surface of the dentale, forms a nearly complete canal for the protection of the cartilage just named. The most solid portion of the bone is that which forms its lower margin, and this part, when articulated with the dentale, forms a direct continuation of the flat submental surface of the latter. Posteriorly it ends in a blunt, rounded, angular process which furnishes attachment to the digastric muscle. Along the external aspect of this heavy portion there run a sharp edge for articulation with the ventral edge of the dentale, and in this, at about its posterior third, is either a deep notch or a complete foramen, the former being much the more usual. This is reinforced by the edge of the dentale and forms the mandibular foramen, through which the mylo-hyoid branch of the fifth nerve reaches the intermandibular region. The remaining, or dorsal part of the bone forms a flattened and much curved wing ending in a sharp upper edge, the rounding outline of which forms a coronoid process which receives the insertion of the temporalis muscle. Along the anterior slope of this process the upper margin is applied to the lower margin of the spleniale.

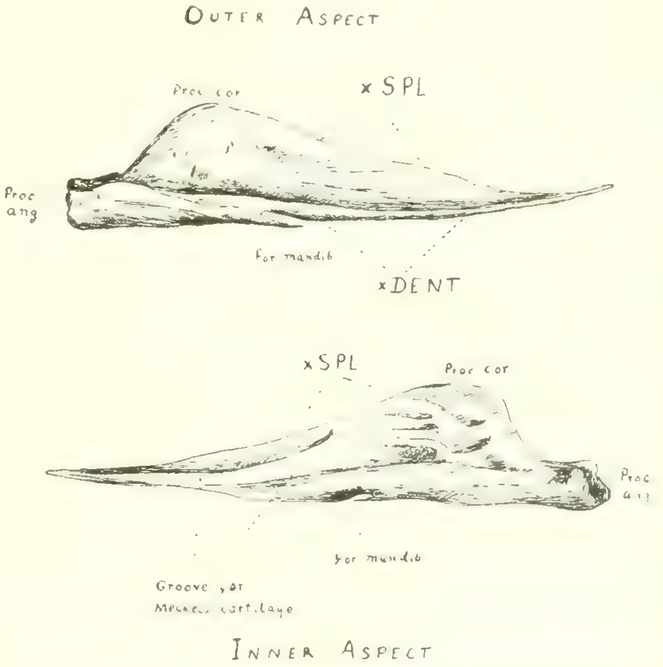


Fig. 20. Two views of right angulare × 3. Contact surfaces with other bones are designated by an x.

This bone is easily oriented, since the more solid base is ventral and the slight curve of the main axis follows the curve of the jaw.

3. SPLENIALE. Next to the operculum of the otic capsule, this is the smallest bone of the skull, and by a singular coincidence, many authors have given it the name "oper-

culare," thus producing a confusion of terms. The spleniale is a thin scale of oval shape, presenting a slightly concave inner, and a slightly convex outer surface. Along the side of the former is attached a row of teeth, and the outer surface shows a longitudinal division into an area covered by the dentale and a free area, which contributes a little to the formation of the outer surface of the mandible.

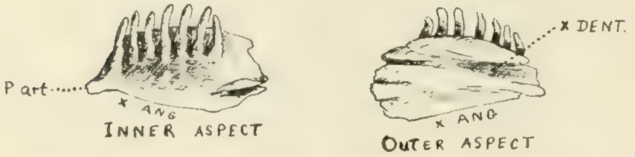


Fig. 21. Two views of right spleniale. × 3. Contact surfaces with other bones are designated by an x. P. ant., processus anterior.

The oval shape and lack of detail of this bone render its orientation difficult, but its outer and inner surfaces are very evident, and in most cases the anterior end is prolonged into a point, while the posterior end is rounded. In its natural position it rests by its lower margin upon the upper edge of the angulare just anterior to the coronoid process, and the ventral half of its outer surface is closely applied to the dentale.

The hyobranchial apparatus. — This consists of a series of sixteen pieces, all but one being entirely cartilaginous, and representing four of the original visceral arches. Their arrangement is so easily seen from plate 65, figure 12, that a verbal description of the parts would seem almost superfluous. The system is seen to contain two median pieces, universally designated as the first and second basibranchials, and referred to the first and second branchial arches respectively, of which they form the middle pieces or copulae. Of these, the second is ossified in the adult and its free posterior end usually terminates in a rounded extremity, although an occasional individual shows a division at the end into a two or three forked form, such as occurs normally in Siren. The hyoid arch, which is attached to the anterior end of the first basibranchial, consists of two pieces, an inner hypohyal and an outer ceratohyal. The first branchial arch is the best developed of all the branchial arches, consisting of two nearly equal pieces, cerato- and epi-branchiale 1, the first of which is directly connected with both the first and second basibranchial and with its opposite. The second branchial arch consists of a smaller epibranchial, and a rudimentary ceratobranchial, reduced to a nodule of cartilage lying upon the inner side of the distal end of the first ceratobranchial. An epibranchial smaller than the previous one is the only remnant of the third branchial arch.

In life the distal ends of the three epibranchials support the external integumental branchiae and furnish attachment for some of their muscles, a circumstance which has often misled investigators as to the true homology of these purely integumental organs, since the location suggests a definite phylogenetic relation to the internal gill system. In the intervals between these epibranchials there occur, even in the adult Necturus, two open gill slits guarded by rudiments of gill rakers, much as in the Axolotl, and as these occur, the one between the first and the second arches, and the other between the second and the third, and consequently in the intervals between the integumental branchiae, the suggestion of connection between the two systems is still more misleading. It may be remembered in this connection that there is a similar external gill upon the shoulder girdle in the Dipnoan, Protopterus, the relation of the two being wholly topographical and without morphological significance. Hence the physiological moments which have developed the external branchiae in this place are plainly the utilization of the gills and their muscular mechanism for support and motion, as well as the currents of fresh water which can be driven through the gill slits in such a way as to bathe the respiratory fringes.

Since the attempt of Fischer ('64) to account for a fourth branchial arch by supposing that the first consists of two fused arches, no good suggestion concerning branchial arches posterior to the third had been made up to about ten years ago, since when a series of investigations by Gegenbaur (29'), Göppert ('94), and myself ('92), have rendered it probable that the laryngo-tracheal cartilages of Amphibia are modified portions of the fifth arch, perhaps the epibranchials. A fourth arch, attached to the hyobranchial apparatus, is present in several of the lower Urodeles, (Siren, Amphiuma, Cryptobranchus), and its apparent absence in Necturus has awakened some little speculation. The rudiment of this was finally discovered by Göppert, who found it to consist of a raphe of connective tissue, separating two muscles normally belonging to the branchial system, and in which, in the larva, he discovered a few cartilage cells. This view I can corroborate by investigations upon the same point at the same time, and which had led me independently to the same conclusions previous to the appearance of the work of Göppert. This raphe is given in the figure referred to (pl. 65, fig. 12), and there can now be little doubt that it represents the missing fourth epibranchial. Concerning the structure of the metamorphosed fifth branchial arches (laryngo-tracheal cartilages), they consist normally of a single pair of somewhat curved pieces, applied to the sides of the glottis and short trachea, and were first described by Henle under the name of cartilago lateralis. They are individually very variable and often have notches, foramina, or detached pieces, but consist essentially of an anterior flat piece in the form of a triangle, from the posterior internal angle of which depends a curved tracheal process extending posteriorly. A more careful description of these cartilages and figures of several varying forms are given in the author's article on the amphibian larynx ('96).

Suspensorial relations of the hyoid.— The distal end of the ceratohyal enters into a ligamentous connection with various parts of the skull and mandible and thus bears a close relation to the suspensorial apparatus of the mandible, a region which has such an important morphological bearing that a description of it is worthy of special consideration. Huxley ('**74**) was the first to describe carefully this region in Necturus, and according to this author there are three important ligaments in this region: (1) a mandibulo-hyoid between the angular process of the mandible and the distal end of the ceratohyal; (2) a hyo-suspensorial between this latter point and the quadrate; and (3) a suspensorio-stapedial, from the quadrate to the operculum. A series of dissections of several very large individuals, under the most favorable conditions as to preservation, has led me to modify somewhat the account given by Huxley, and to substitute the interpretation graphically given in the accompanying figure (fig. 22). The distal end of the ceratohyal is traversed by a deep groove in which runs the tendon of the digastric muscle, and which forms an outer and an inner lip. At the posterior end of the inner lip there is developed a rather prominent process. There are two distinct mandibulo-hyoid ligaments, external and internal, the one from the outer lip of the digastric groove to the lower corner of the angular process, and the other from the inner lip of the groove and from its process to the angular process just above the attachment of the other. The hyo-suspensorial ligament is a narrow but very strong and distinct band extending between the middle of the inner lip of the digastric groove and the outer side of the quadrate bone. In spite of repeated careful dissections I could not find any definite "stapedio-suspensorial" ligament, but instead of this a rather soft and somewhat indefinite sheet of connective tissue extending along the entire inner lip of the ceratohyal and attached along a corresponding length of the skull, involving the operculum, a bit of the cartilaginous otic capsule, and a part of the quadrate. At its posterior edge its fibers become stronger and thicker, and thus resemble a hyo-stapedial ligament, but as this part is directly continuous with the remainder of the sheet and is by no means as definite as the other genuine ligaments, it can hardly be described as a definite part. This loose sheet of connective tissue, which, as a matter of fact, adheres very closely to the columellar process of the operculum, is undoubtedly the

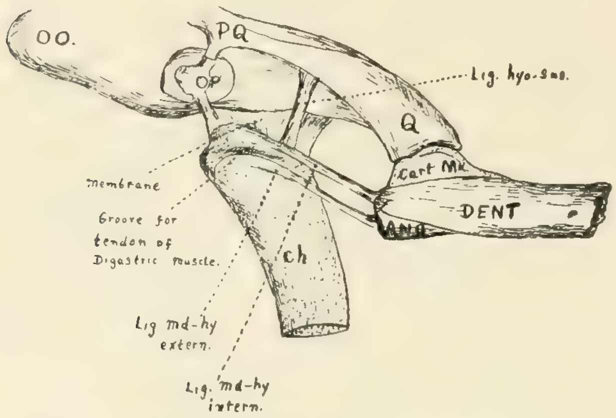


Fig. 22. Relations of suspensorium, jaw and hyoid, taken from the right side. × 3. Lig. hyo-sus., ligamentum hyo-suspensoriale; lig. md.-hy. extern., ligamentum mandibulo-hyoideum externum; lig. md.-hy. intern., ligamentum mandibulo-hyoideum internum; membrane, that between skull and ceratohyal, forming posteriorly a thickened band, extending between operculum and ceratohyal.

part described by Huxley as the stapedio-suspensorial ligament. Certainly no definite ligament, the fibers of which extend between the operculum and the quadrate, can be demonstrated.

In this connection it is interesting to compare the work of other writers on the subject, who have naturally been influenced by the description given by Huxley. W. K. Parker (**'77**, pl. 28, fig. 5) has figured this region in detail in Proteus. This shows the same broad connective tissue band first described, but no definite stapedio-suspensorial ligament. This band, which appears identical with that which I have described in Necturus, is lettered "st. sl.," but no mention is made of it in the text. The two other ligaments are as in Necturus, if one counts the two mandibulo-hyoid ligaments as one. Wiedersheim (**'77**) accepts Huxley's statements and quotes them (paraphrased, p. 435). He speaks of a lig. stapedio-suspensoriale in Proteus, but in his figure 19, in which he refers to this ligament as "Prop," he really points out the bony connection between operculum and paraquadratum, showing that he has confused the two, perhaps for the moment. His figure of Proteus is in reality like W. K. Parker's, and well expresses the condition in Necturus.

The Free Sense Capsules.

The nasal capsules and the sclera of the eyes receive a more or less complete reinforcement of cartilage, which is structurally a skeletal part, and may be considered under the heading given above.

The nasal capsules are somewhat in the shape of round-bottom flasks with necks curved outwards, and they lie upon the sides of the anterior angle of the skull, extending from the alveolar processes of the premaxillaries to the antorbital processes. The nostrils or anterior nares appear at the end of the outwardly curved necks and are hence divergent from one another and situated upon the sides of the blunt snout with a wide interspace. The posterior nares lie underneath, near the rounded posterior end, and in close connection with the anterior margin of the antorbital processes which are curved somewhat around them. The sides and roof of each capsule are covered by a delicate reticular or fenestrated cartilage of a soft consistency and rather difficult of demonstration as cartilage.

A very similar structure is found in Proteus, where it was first described by Leydig. in 1853, (quoted by Wiedersheim, **'77**) and the form in Necturus appears to have been first shown by Wiedersheim, in 1877, who both describes and figures it with great clearness, but may perhaps have given in his drawing somewhat too great regularity to the fenestrations. Both Huxley (Necturus) and W. K. Parker (Proteus) appear to have entirely overlooked the structure or at least not to have recognized its skeletal nature. In the adult it appears like a shell covering the dorsal half of the capsule, its edge being entire and running along the lateral outline. Its surface is perforated by openings in the form of irregular parallelograms approximately arranged in two longitudinal rows and converting the entire structure into a delicate cartilaginous network. At the anterior end a narrow loop appears to extend across the ventral side, thus enclosing the nostril. By an examination of the larvae it would seem that this structure at first consists of a single longitudinal rod applied to the inner side of the capsule, after which transverse rods develop between the folds of the nasal mucous membrane. Miss Platt (**'97**) has given a brief description of this in a larva of 46 mm., and Winslow (**'98**) has both described and figured it at the same stage. In the printed description of both authors the transverse lateral processes develop or project directly from the main longitudinal rod, but in Winslow's figure 16 certain of the transverse rods appear entirely separate from the longitudinal one as though they had arisen independently of it. The later development of this capsule and the manner in which the original elements finally weave themselves into the complicated network seen in the adult, are points which have not as yet been investigated.

The term "optic capsule" seems almost too formal a word for the thin cartilaginous ring which appears in the sclera and surrounds the eye. It is hardly demonstrable to the unaided eye but is clearly seen in sections. Miss Platt found it in a larva of 46 mm. to be "three cells wide and one cell deep," and in a small adult, of which I have sections, it is from about 15 to 20 cells wide and about 4 cells deep in the thickest portion, tapering towards each edge. The drawing of it given in plate 64, figure 6, is purely diagrammatic and obtained from sections, as I have not succeeded in preparing an eye so that it could be seen directly. According to Miss Platt, both nasal and optic capsules arise independently.

The Teeth.

The teeth of Necturus are arranged in two parallel rows in the upper jaw and in a single row in the lower, those of the latter fitting into the interval between the two rows of the former, their mutual arrangement being such that the teeth on the dentale oppose those of the vomer, those on the spleniale oppose those on the palato-pterygoid, while the premaxillary teeth form an unbroken outer row shutting over all the rest. At the juncture between the vomerine and palato-pterygoid teeth of the inner, upper row, and again between the dental and splenial teeth of the lower row there are slight breaks in the continuity of the rows, and usually a perceptible diastema or gap. Several of the authors have given a definite number of teeth for each dentigerous bone, and Cope ('89) has even employed the number of teeth as a diagnostic between species, but as a matter of fact the number is quite inconstant, and it seems probable that the rows are added to upon their outer or posterior ends as the animals become older. The result of a series of enumerations of different specimens may be given in the following tables.

TABLE A.

Teeth enumerated in entire specimens.

Designation of specimen.	Side.	Premaxillary.	Vomer.	Palato-pterygoid.	Dentale.	Splenale.	Total on a side.	Total teeth.
A	Rt	12	12	5	14	6	49	99
	L	12	13	5	15	5	50	
B	Rt	10	10	5	14	6	45	93
	L	11	11	6	15	5	48	
C	Rt	10	10	5	14	6	45	93
	L	11	11	6	15	5	48	
D	Rt	9	10	6	13	5	43	87
	L	9	11	6	13	5	44	
E	Rt	14	15	8	15	7	59	121
	L	15	15	8	16	8	62	
F	Rt	12	13	8	18	—[1]	—	—
	L	12	12	7	17	—[1]	—	

TABLE B.

Teeth counted in isolated bones.

	PMX.	V.	PPT.	DENT.	SPL.
	14	14	7	20	7
	14	13	8	18	7
	13	13	8	17	7
	15	15	9	16	7
	15	17	8	17	6
		16	6	16	7
		15	6	18	
		17		17	
average[3]	12.5 –	13.0	6.6	15.9 +	6.2 –

---

[1] These small bones were unfortunately lost in this specimen.

[2] The specimens which furnished these isolated bones were generally larger than those used for Table A, which accounts for the greater number of teeth.

[3] In this average are included the statistics from both tables.

The teeth are pleurodont, *i. e.*, situated upon the inner side of the tooth-bearing ridge, and possess a root and a crown, the division between the two being coincident topographically with the edge of the bone upon the outside of a row of teeth. Thus the root, which is formed simply of bone substance, and is unprotected by enamel, is guarded by the ridge of bone, while the enameled crowns project beyond this protection. The root is made of a hard bony substance or dentine, and is directly continuous with the bone which bears it, arising from it by two lateral supports, which leave between them the characteristic hollow seen in all of the figures that represent teeth as seen from the inner aspect. Each hollow is really a foramen, which forms the entrance to the pulp canal of the crown and serves in life to transmit the special nerves and blood vessels which supply the tooth. The crown is in the shape of a slender cone, with a tip that is often set off a little from the rest by a slight constriction. The apex is pointed and slightly recurved, and is colored at the very point a deep amber color, similar to that found upon the exposed outer surface of the incisors of beavers and many other rodents.

Comparison of Nomenclature.

That the numerous authors who have written upon the Urodele skull have not been in accord with regard to the nomenclature of the elements concerned is to be expected when we consider both the time covered by their investigations, and the fact that grounds for an accurate homologizing of the parts have been sadly lacking, especially previous to the epoch making years of the '60's and '70's. An attempt to arrange the synonyms used by various authors in designating the parts of the skull of Necturus and a few allied forms is given in the following table. The two last columns give respectively the terms used in this work and the abbreviations by which they are designated in the figures.

TABLE C.

Comparison of nomenclature of important parts of the skull.

HYRTL, 1865 (Cryptobranchus)	HUXLEY, 1874	WIEDERSHEIM, 1877	W. K. PARKER, 1877 Proteus	GAUPP, 1895 (also frog, 1896.)	WILDER, 1903	Abbreviations.
ossa frontalia[1]	frontal (bones)[1]	frontalia	frontals		frontal	F
ossa parietalia	parietal (bones)	parietalia	parietals		parietal	P
os sphenoideum basilare	parasphenoid	parasphenoid	parasphenoid	parabasale	parabasal	PB
ossa intermaxillaria	premaxillae	premaxillaria	premaxillaries		premaxillary	PMX
os maxillare superius (?)	vomers	vomer[1]	vomers		vomer	V
os pterygoideum [Here without the palatine.]	palato-pterygoid	pterygo-palatinum	pterygo-palatines		palato-pterygoid	PPT
ossa mastoidea	squamosals	tympanicum *seu* squamosum	squamosals	paraquadratum[2] tympanicum	paraquadrate	PQ
ossa petrosa	pro-otic (ossifications)	pro otische Verknöcherung s. regio pro-otica petroso-occipitale	pro-otic		pro-otic	PO
	epi-otics including opisthotics	regio epi-otica regio opisthotica	epi-otic including opisthotic		opisthotic	OO
os occipitis partes laterales	exoccipitals	regio occipitalis lateralis	feebly developed occipital floor		exoccipital	EXO
os tympanicum	quadrate (ossification)	kleine, am Ende des Quadrat-knorpels auftretende Verknöcherung	suspensorium, ossified part		quadrate	Q
operculum	stapes	operculum mit columella	stapes		operculum	O
maxilla inferior	dentary	dentale	dentary		dentale	DENT
		angulare	articulare		angulare	ANG
	splenial	operculare			spleniale	SPL
lingulae cartilagineae	trabeculae	Trabekel; Schädelbalken	trabeculae		trabeculae	tr
cartilago ethmoidea	internasal fusion of trabeculae	unpaare Platte	internasal cartilage		internasal plate	in
		vorderste Ausläufer der Trabekel	trabecular cornua		rostral processes	r
	autorbital processes	Antorbital-fortsatz	ethmo-palatine element, or antorbital element		antorbital process	ao
saccus vestibuli	auditory capsules	Labyrinth-kapsel; pars cartilaginea	ear capsules		otic capsule	ot
parva lamina cartilaginea ossis occipitis		supra-occipitale Knorpel-platte	super-occipital band		supra-occipital arch	so
os occipitis — pars basilaris		basi-occipitale Knorpel-platte	an ossified bridge of cartilage		basi-occipital arch	bo

[1] The form given here is taken direct from the text of the author cited, and may be in one case the plural and in another the singular form, or may be used as an adjective. These differences are of course without significance.

[2] Gaupp, in suggesting the term "paraquadratum" leaves open a possible, or even probable, homology with the tympanicum of mammals, and in the frog has so named the corresponding bone.

THE APPENDICULAR SKELETON.

Shoulder Girdle.

The shoulder girdle consists of a pair of thin plates, almost entirely cartilaginous, wrapped about the sides of the body near the anterior end of the trunk, and entirely disconnected from other parts of the body skeleton and from one another. At about the middle of each plate is situated the glenoid fossa for the reception of the head of the humerus, and from this as a center there radiate three processes or lobes, one extending dorsally and two ventrally. The dorsal or scapular extension is narrow at its origin but broadens out towards its free end into a hatchet-shaped piece which extends as far dorsally as the transverse processes of the vertebrae. The narrow part of this extension becomes ossified to form a scapula, in shape something like the diaphysis of a shaft bone, with a constricted middle portion and two broadened ends; beyond this ossification the hatchet-shaped piece remains as a cartilaginous suprascapula. Of the two ventral extensions, the anterior, or procoracoid, is long and narrow and directed nearly anteriorly, while the posterior, or coracoid, forms an almost circular flat plate closely applied to the myotomic muscles on the ventral side of the thoracic region and extends so far beyond the median line that the coracoid of one side considerably overlaps the other, the left being usually the ventral or superficial one.

The cartilage, which is thin in most regions, is considerably thickened about the glenoid fossa both to strengthen the region and to allow sufficient depth for the reception of the head of the humerus. Externally, the thickened portion forms a definite ridge or lip nearly surrounding the fossa, being deficient only for a small space upon the anteromedial aspect.

Midway between the glenoid fossa and the re-entrant angle formed between procoracoid and coracoid is seen a small foramen coracoideum through which passes the supracoracoid nerve on its way to supply the muscles upon the ventral surface of the shoulder girdle. C. K. Hoffmann has pointed out that in the Anura this nerve lies in the interval between the procoracoid and coracoid, while here it bores through the cartilage, and that the result is brought about in the former case by a deepening of the incision between the two elements in question far enough to include the region of the foramen.

When the shoulder girdle is in its proper relationship to the body, the coracoid extends from the second to the fourth myocomma, and hence the largest of the sternebra, the one connected with the fourth myocomma, is situated exactly at the point at which the posterior margins of the two coracoids diverge from one another, a relation precisely similar to that of the sternal plate of the higher Urodela and of the arciferous Anura (*e. g.*, Bombinator). This gives a suggestion of homology between the later amphibian sternum and the sternebrum of the fourth myocomma alone, the shape and extent of which frequently remind one of the well known rhomboid plate of such a form as Salamandra.

The procoracoid extends anteriorly as far as the first myocomma and its free anterior end is frequently covered by the transverse fold formed by the posterior border of the intermandibular muscle (M. intermaxillaris of authors).

Pelvic Girdle.

The pelvic girdle consists of a flat ventral plate, the pubo-ischium, and two lateral pieces, the ilia, attached to the sacral vertebra by means of a pair of ribs. The ventral plate has an elongated pentagonal outline similar to that shown by the skull but with its longitudinal axis still more prolonged. The anterior median angle is especially tapering and extends along the mid-ventral line of the abdomen but shows no trace of an epipubic cartilage (cartilago ypsiloides) as in so many Urodeles. The ilia are attached along the posterior lateral sides and at their bases are situated the acetabula for the reception of the heads of the femora. As in the case of the skull, the posterior margin is slightly incurved and its outer angles (corresponding in position to the mastoid processes of the opisthotics) are somewhat prolonged and tuberculate, forming the tuberosities of the ischia. At about the middle of the pubo-ischium are seen two small obturator foramina which may be used as indicative of the boundary between the pubic and ischiadic elements which are here otherwise unmarked. A pair of osseous areas situated in the posterior half, and which develop and increase in size during growth, plainly represent the osseous ischia. The growth of these is well marked by concentric lines. The middle portion of the ilium is also ossified, the bone being a little curved and with a rounded dorsal, and a broad and flat ventral end.

The ventral face of the pubo-ischium shows a slight muscular ridge along the middle line, and the dorsal or inner face is considerably excavated to form a pubo-ischiadic fossa for the accommodation of some of the viscera. The floor of the acetabulum is usually broken through by an acetabular foramen which leads into this last mentioned fossa.

The lateral view (pl. 65, fig. 13) shows the manner in which the ilium is attached to the sacral rib. Instead of meeting end to end and forming a definite joint, the cartilaginous ends of the two are prolonged and tapering and are applied to the sides of one another and held in place by firm connective tissue. The relations of this attachment to the vertebrae have been considered above under the vertebral column. In two cases which I have seen, a second ligamentous attachment appeared upon one side, extending from the rib previous to the sacral rib to the dorsal end of the ilium; and in one of these which I have had the opportunity of examining more closely, the sacral rib on the right is normal and attached to what is probably the 19th vertebra, while the sacral rib upon the left side proceeds from the next posterior vertebra (20th). In addition to this, a strong but narrow ligament proceeds from the free end of the previous rib (19th) and inserts upon the dorsal end of the ilium anterior to the attachment of the sacral rib. As this fragment came from a student's preparation, the remainder of which had been lost, the exact determination of the vertebrae cannot be made, but judging from the other cases of oblique attachment which have been reported, the numbering is undoubtedly as given. This case resolves itself into one of "oblique attachment," such as have been reported by G. H. Parker, Waite, and Bumpus, the obliquity being dextro-sinistral (see above, under *Vertebral Column*).

The Free Limbs.

The serial homology between the fore and hind limbs in Necturus is very striking, and in so primitive an animal, perhaps the most primitive one possessing a cheiropterygium, points to a fundamental similarity of origin. It is thus of greater morphological interest than correspondences in such modified structures as the paddles of Ichthyosaurus where it is likely that the similarity is a secondary modification due to a similar method of use. This resemblance, which is apparent externally, is still more emphasized by the skeletal parts, and it seems incongruous to find such similar free limbs attached to such different girdles. Each limb terminates in four digits, the lost member being generally considered to be the first, and the phalangeal formula, 2–2–3–2, is the same in both manus and pes.[1]

With the exception of carpus and tarsus, which are wholly cartilaginous, the limb bones of the adult consist each of a bony shaft running through the middle, and two cartilaginous epiphyses, a slight exception being the terminal phalanges which are without epiphyses at the distal end. The shaft, or diaphysis, ossifies perichondrially, as always in the Amphibia, and forms a tubular sheath of bone, thick and constricted in the middle of its length and tapering at the ends to thin edges, the whole mass being something like the centrum of a biconcave vertebra considerably prolonged in the direction of its length. The epiphyses always remain purely cartilaginous, and never obtain calcareous deposits as in the frog.

---

[1] On this point Cope ('**89**, p. 25–28) seems to have made a singular mistake, giving the phalangeal formula for *N. maculatus* as 1–3–3–2 for the manus, and 1–2–2–2 for the pes. For the rare Carolina form, *N. punctatus*, he gives the formula 2–2–3–2 for both limbs, which corresponds to the normal condition in *N. maculatus* and is undoubtedly characteristic of the entire genus.

The limbs when in the normal resting or swimming position are directed backwards, and are held in such a way that in the hind limbs the soles face inwards, while in the fore limbs the dorsal surface of the manus is ventral, and the palm dorsal. This is apt to cause considerable difficulty in orienting the parts, but if the action of the limbs be watched in a living animal it will be seen that this position is due, not so much to a torsion, as to a swinging of the entire limb at the shoulder. The position assumed by the fore limb is the easier to understand, and in this it is evident that the limb when extended forward as in walking, rests with the palm down and the dorsal surface of the manus up, but that when the entire limb is swung from the shoulder so as to change its direction and point backwards, the positions of palm and dorsum are necessarily reversed. In the hind limb there is some tendency to counteract this by a torsion of the limb about its own axis and thus in a trailing hind foot the sole is turned somewhat inward.

Humerus.— The humerus, like the other long bones of the limbs, consists of an osseous shaft and two cartilaginous epiphyses. The usual cylindrical shape is retained only at the middle while the ends are both strongly flattened, and at right angles to one another, the proximal end being flattened laterally, and the distal end dorso-ventrally. The most prominent part of the proximal epiphysis is the head, which fits into the glenoid fossa of the shoulder girdle and forms the characteristic ball-and-socket joint. It is subspherical in shape, and is slightly affected by the general flattening of the entire region. Its ventral face is prolonged into a sharp ridge which is continued by the osseous diaphysis and forms one of the most distinctive features of the bone. This is the crista ventralis (crista deltoidea of Ecker) and serves for the insertion of most of the ventral shoulder muscles. This crest is highest near the junction of cartilage and bone and rapidly recedes, so that at the middle of the diaphysis no trace remains.

The distal end, which is broadened laterally and flattened dorso-ventrally, bears an extensive median furrow running around the end and up both surfaces, and dividing it into two masses which may be distinguished as the external (lateral) and the internal (median) condyles, although they include parts which in higher forms are distinct from the condyles themselves. The external condyle is somewhat the larger and is ball-shaped, fitting into the socket in the head of the radius. It also serves as a point of origin for the extensor muscles of the forearm and hand. Having these two functions, it plainly corresponds to both the external condyle and the capitulum of higher animals (epicondylus medialis and eminentia capitata of the frog; Gaupp).

The internal condyle is more nearly the exact homologue of the part of that name in higher forms as it gives origin to the flexor muscles of forearm and hand, but does not participate as directly in the formation of the elbow joint. The groove between the two condyles lies in the greater sigmoid notch of the ulna, and the olecranon of the ulna and the capitulum of the radius fit respectively into its dorsal and ventral continuations during forced extension and flexion of the forearm. These slight grooves or depressions, of which the ventral is, perhaps, a little stronger than the dorsal, are thus the first suggestions of the olecranar and cubital fossae which develop in higher forms.

The humerus is distinguished from the femur by its sharp crista ventralis which projects farther than that of the femur and is differently shaped. This same feature, which marks the ventral side, and the large and spherical external condyle serve to orient the humerus.

Femur.— The general shape of the femur is like that of the humerus, but without much flattening at the proximal end. Here it shows two projections for muscular attachment: (1) a distinct process, mostly formed by bone, but tipped with a cartilage which in the adult is independent of the main epiphysis, and (2) a ridge or crest upon the side of the head, involving also a part of the shaft. It is somewhat difficult to compare these two distinct features with the single crista ventralis of the humerus, but in accordance with position it would seem that the bony process corresponds most closely with that part, and may thus bear the same name, while the ridge which lies more upon the external lateral aspect may be designated as the crista lateralis. As this crest is similar in appearance, though not in position, to the proximal cartilaginous part of the crista ventralis of the humerus, it is possible that these two parts found in the femur correspond to the single process of the humerus, and that in the former a difference in motion and consequently in muscular insertion has separated the two parts and diverted one of them from its original position. Such an explanation is, however, not in accord with the almost universally greater differentiation of the anterior limb, and one would expect to find in the femur the more primitive condition. Hoffmann distinguishes in the Urodeles a single projection referred to as crista femoris, a name applied by Gaupp to a similar part in the frog, but the femur of this latter animal is so unlike that of Necturus that homologies of parts are uncertain. It hence seems better to refer to the two processes found in Necturus by the two terms given above, crista ventralis and crista lateralis, terms which accurately express the position of the parts, and one of which suggests a justifiable homology with the humerus of the same animal.

The distal joint is imperfectly divisible into the external and internal condyles, although there is no distinct groove between them. The internal condyle is larger and longer and serves as the main point of origin for both flexor and extensor muscles of the lower leg and foot. The smaller external condyle articulates with the proximal end of the fibula.

The osseous crista ventralis, separated from the head by a notch, is sufficient to distinguish femur from humerus and to mark the ventral side of the bone. This and the more projecting internal condyle of the distal epiphysis will complete the determination.

Antibrachium and manus; crus and pes.— These parts in the two limbs are almost indistinguishable from one another, as may be seen by a comparison of figures 14 and 15 (plate 66), which were drawn from the right anterior and posterior limbs of the same individual by the aid of a camera lucida. Corresponding to a difference in use of elbow and knee, the proximal ends of ulna and radius are different from those of tibia and fibula, but otherwise the parts correspond as closely as do consecutive parapodia of a polychaetous Annelid.

The ulna shows a greater sigmoid notch and the radius a capitulum, both for the reception of parts of the distal epiphysis of the humerus. Furthermore, these bones are a little longer than are the tibia and fibula. Carpus and tarsus are exact duplicates in the two limbs and consist of two proximal bones, a centrale, and three bones of the distal row. In the proximal row the intermedium is fused with the outer element (ulnare or fibulare), leaving between them a foramen for the transmission of an artery.[1] In the distal row, digits II and III have each a distinct element, while those corresponding to IV and V are fused. Four digits, II–V, are represented in each case, each with a well developed metacarpal or metatarsal and nine phalanges, three in the fourth digit and two in each of the others. Three phalanges in the third digit, also, is a not uncommon anomaly.

LITERATURE.

Bumpus, H. C.

'97. A contribution to the study of variation. (Skeletal variations of *Necturus maculatus* Raf.) Journ. of morphol., vol. 12, p. 455–484, pl. A–C.

Cope, E. D.

'89. The Batrachia of North America. Bull. U. S. nat. mus., no. 34, 525 pp., 119 figs., 86 pls.

Fischer, J. G.

'64. Anatomische abhandlungen über die Perennibranchiata und Derotremen. 4°. Taf. 1–8.

Gadow, H.

'97. On the evolution of the vertebral column of Amphibia and Amniota. Phil. trans. royal soc. London, vol. 187, series B, p. 1–57, fig. 1–56.

Gaupp, E.

'92. Beiträge zur morphologie des schädels. 1. Morphol. arbeiten, bd. 2, p. 275–481, taf. 13–16.

'94a. Beiträge zur morphologie des schädels. 2. Das hyo-branchial skelet der Anuren und seine umwandlung. Morphol. arbeiten, bd. 3, h. 3, p. 399–438, fig. 1, taf. 18–19.

'94b. Beiträge zur morphologie des schädels. 3. Zur vergleichenden anatomie der schläfengegend am knöchernen wirbelthier-schädel. Morphol. arbeiten, bd. 4, h. 1, p. 77–130, taf. 6–7.

'96. Die anatomie des frosches. (New edition of the well known book of Ecker and Wiedersheim.) 1896.

Gegenbaur, C.

'92. Die epiglottis. Vergleichend-anatomische studie. 4°: p. 1–69, fig. 1–14, taf. 1–2.

---

[1] The artery in the hand which runs through the foramen carpale is the art. cubitalis which thus reaches the dorsal surface and is distributed to the digits. In the foot a similar function is performed by the continuation of the art. femoralis.

Göppert, E.

'94. Die kehlkopfmuskulatur der Amphibien. Morphol. jahrb., bd. 22, h. 1, p. 1–78, fig. 1–9, taf. 1–2.

'96. Die morphologie der amphibienrippen. Festschrift zum siebenzigsten geburtstage v. Carl Gegenbaur, bd. 1, p. 393–435, fig. 1–10, taf. 1–2. Leipzig.

'98. Der kehlkopf der Amphibien und Reptilien. 1 Theil: Amphibien. Morphol. jahrb., bd. 26, h. 2, p. 282–329, fig. 1–5, taf. 8–11.

'01. Beiträge zur vergleichenden anatomie des kehlkopfes und seiner umgebung, mit besonderer berücksichtigung der Monotremen. Aus Semon: Zoologische forschungsreise in Australien und dem Malayischen archipel. 4°: p. 535–634, fig. 1–52, taf. 17–21.

Hoffmann, C. K.

'73 '78. Amphibien. In Bronn's Klassen und ordnungen des thierreichs, bd. 6, abth. 2. Leipzig u. Heidelberg.

Huxley, T. H.

'74. On the structure of the skull and of the heart of *Menobranchus lateralis*. Proc. zool. soc. London, 1874, p. 186–204, pl. 29–32.

Hyrtl, J.

'65. *Cryptobranchus japonicus*. Vienna.

Parker, G. H.

'96. Variations in the vertebral column of Necturus. Anatom. anzeiger, bd. 11, p. 711–717, fig. 1–2.

Parker, W. K.

'77. On the structure and development of the skull in the urodelous Amphibia. Part 1. Phil. trans. royal soc. London, vol. 167, pt. 2, p. 529–597, pl. 21–29.

(In the above article, the description of Proteus is the one of especial value in this place.)

Platt, J. B.

'97. The development of the cartilaginous skull and of the branchial and hypoglossal musculature in Necturus. Morphol. jahrb., bd. 25, h. 3, p. 377–464, pl. 16–18.

Stöhr, Ph.

'80. Zur entwicklungsgeschichte des urodelenschädels. Zeitschr. f. wissenschaftl. zool., bd. 33, h. 4, p. 477–526, taf. 29–30.

Waite, F. C.

'97. Variations in the brachial and lumbo-sacral plexi of *Necturus maculosus* [= *maculatus*] Rafinesque. Bull. mus. comp. zool., vol. 31, p. 69–92, pl. 1–2.

Wiedersheim, R.

'77. Das kopfskelet der Urodelen. Morphol. jahrb., bd. 3, h. 3, p. 352–448, fig. 1, taf. 19–23.

Wilder, H. H.

'92. Studies in the phylogenesis of the larynx. Anatom. anzeiger, bd. 7, no. 18, p. 570–580, fig. 1–3.

'96. The amphibian larynx. Zool. jahrb., abtheil. f. anat. u. ontog., bd. 9, h. 2, p. 273–318, fig. A–D, pl. 19–21.

Winslow, G. M.

'98. The chondrocranium in the Ichthyopsida. Tufts college studies, no. 5, p. 147–201, pl. 1–4.

EXPLANATION OF PLATES.

(The outlines of all the figures were drawn with a camera, three times the natural size in the majority of the cases. Since, however, the originals varied considerably in size, the resulting figures cannot be considered as proportionate to one another. The figures of the chondrocranium, for example (pl. 63, figs. 4, 5), were drawn from a very small specimen and enlarged four times, but the resulting figures are almost exactly comparable with those of the entire skull (pl. 63, figs. 2, 3) drawn from a medium sized specimen at a magnification of but three diameters. A large skull at two diameters would give about the size of figures 2 and 3.)

ABBREVIATIONS USED.

(The abbreviations given in the following list include those used in the figures, as well as those employed in the text at various places.)

1. Bones.

A — atlas.
ANG — angulare.
BB — basibranchiale 2.
CS — costa sacralis.
DENT — dentale.
EXO — exoccipitale.
F — frontale.
FB — fibula.
FM — femur (diaphysis).
H — "1st haemal arch vertebra" (see text).
HM — humerus (diaphysis).
IL — ilium.
IS — ischium.
MC — metacarpalia.
MT — metatarsalia.
OO — opisthoticum.
OP — operculum.
P — parietale.
PB — parabasale.
PH — phalanges.
PMX — praemaxillare.
PO — prooticum.
PPT — palato-pterygoideum.
PQ — paraquadratum.
Q — quadratum.
R — radius.
S — sacrum.
SC — scapula.
SPL — spleniale.
T — tibia.
UL — ulna.
V — vomer.

2. Other Designations.

Abbreviation Name.	*Location.*
a. b–o. — arcus basi-occipitalis.	
art. — articulare (Meckel's cartilage).	
a. s–o. — arcus supra-occipitalis.	
b. b. 1. — basibranchiale 1.	
br. — bronchus.	
c. — carpalia.	
caps. nas. — capsula nasalis.	
caps. opt. — capsula optica.	
caps. ot. — capsula otica.	
cart. lat. — cartilago lateralis.	
cart. Mk. — cartilago Meckelii.	
c. b. 1–2. — ceratobranchiale 1 et 2.	
cent. — centrale.	
c. h. — ceratohyale.	
cond. ext. — condylus externus.	H and FM.
cond. int. — condylus internus.	H and FM.
cond. oc. — condylus occipitalis.	EXO.
cor. — coracoideum.	
cr. lat. — crista lateralis	FM.
cr. mus. — crista muscularis.	Pelvic girdle.
cr. temp. — crista temporalis.	F.
cr. ventr. — crista ventralis.	H and FM.
e. b. 1–4. — epibranchialia 1–4.	
epiph. c. s. — epiphysis costae sacralis.	
epiph. il. — epiphysis ilii.	
f. acet. — foramen acetabulare.	
f. carp. — foramen carpale.	
f. cor. — foramen coracoideum.	
f. mand. — foramen mandibulare.	
f. obtur. — foramen obturatorium.	
f. sty.-m. — foramen stylo-mastoideum.	
f. tars. — foramen tarsale.	
fib. — fibulare.	
fn. oval. — fenestra ovalis.	

Abbreviation. Name.	*Location.*
foss. acet.— fossa acetabularis	
foss. glen. - fossa glenoidalis.	
foss. olec.— fossa olecrani.	
foss. pub.-isch.— fossa pubo-ischiadica.	
h.-h — hypohyale.	
int.— intermedium.	
isch.—ischium (cartilaginous).	
isth.— isthmus.	
lig. hyo-sus,— ligamentum hyo-suspensoriale.	
lig md-hy ext.— ligamentum mandibulo hyoideum externum.	
lig. md hy. int.— ligamentum mandibulo hyoideum internum.	
marg. ventr. — margo ventralis.	Of anterior naris.
nar. ant.— naris anterior.	
p. a-l.— proc. antero-lateralis.	P.
p. a-m.— proc. antero-medianus.	P.
p. a-o.— proc. antorbitalis.	
p. ang.— proc. angularis.	ANG.
p. ant.— proc. anterior.	SPL.
p. artic.— proc. articularis.	Q.
p. asc.— proc. ascendens.	q.
p. colum.— proc. columellaris.	OP.
p. cor.— proc. coronoideus.	ANG.
p. mast.— proc. mastoideus.	oo.
p. oo.— proc. opisthoticus.	P.

Abbreviation. Name.	*Location.*
p. operc.— proc. opercularis.	PQ.
p. orb-sph.— proc. orbito-sphenoidalis	P.
p. ot.— proc. oticus.	Q+q.
p. par.— proc. parietalis.	F.
p. pmx.— proc. premaxillaris.	F.
p. p o. — proc. pro-oticus.	P.
p. pt. — proc. pterygoideus.	q.
p. q.— proc. quadratus.	P.
p. q. d.— proc. quadratus dorsalis.	PO.
p. q. v.— proc. quadratus ventralis.	PO.
p. r.— proc. rostralis.	
p. uncin.— proc. uncinatus.	F.
pc.— procoracoideum.	
ped.— pediculus.	q.
pl. int.-nas.— planum internasale.	
pub.— pubis.	
pul.— pulmo.	
q.— quadratum (cartilage).	
rad.— radiale.	
ss.— suprascapula.	
sym.— symphysis mandibulae.	
t.— tarsalia.	
tib.— tibiale.	
trab.— trabecula.	
trach.— trachea.	
tub. isch.— tuberositas ischii.	
uln.— ulnare.	

PLATE 62.

Figs. 1a, 1b. Vertebral column. × 1½. The view is a dorsal one as far as the sacrum, beyond which it becomes twisted so as to expose the right side of the flattened caudal region. The break between vertebrae 34 and 35 indicates that the detached piece was drawn from a second specimen, but one in which the identity of the vertebrae was known.

A — atlas ; S — sacrum ; H — the first vertebra showing a complete haemal arch.

PLATE 63.

Fig. 2. Dorsal view of skull with nasal capsules removed.

Fig. 3. Ventral view of same.

Fig. 4. Dorsal view of chondrocranium with its cartilage bones.

Fig. 5. Ventral view of same.

PLATE 64.

Fig. 6. Nasal capsule in place ; dorsal view.

Fig. 7. Internal aspect of left mandible.

Fig. 8. External view of same.

Fig. 9. Details of the otic capsule and suspensorium ; ventral view of right side. Some of the parts are slightly separated.

Fig. 10. Dorsal view of suspensorium (quadratum).

Fig. 11. Ventral view of same.

PLATE 65

Fig. 12. Ventral view of head and neck regions, showing visceral arches.

Fig. 13. Lateral view of pelvic girdle, with attachment to vertebral column.

Fig. 14. External lateral view of right humerus.

Fig. 15. External lateral view of right femur.

PLATE 66

Fig. 16. Ventral view of right shoulder girdle.

Fig. 17. Lateral view of right shoulder girdle.

Fig. 18. Forearm and manus—dorsal view of right.

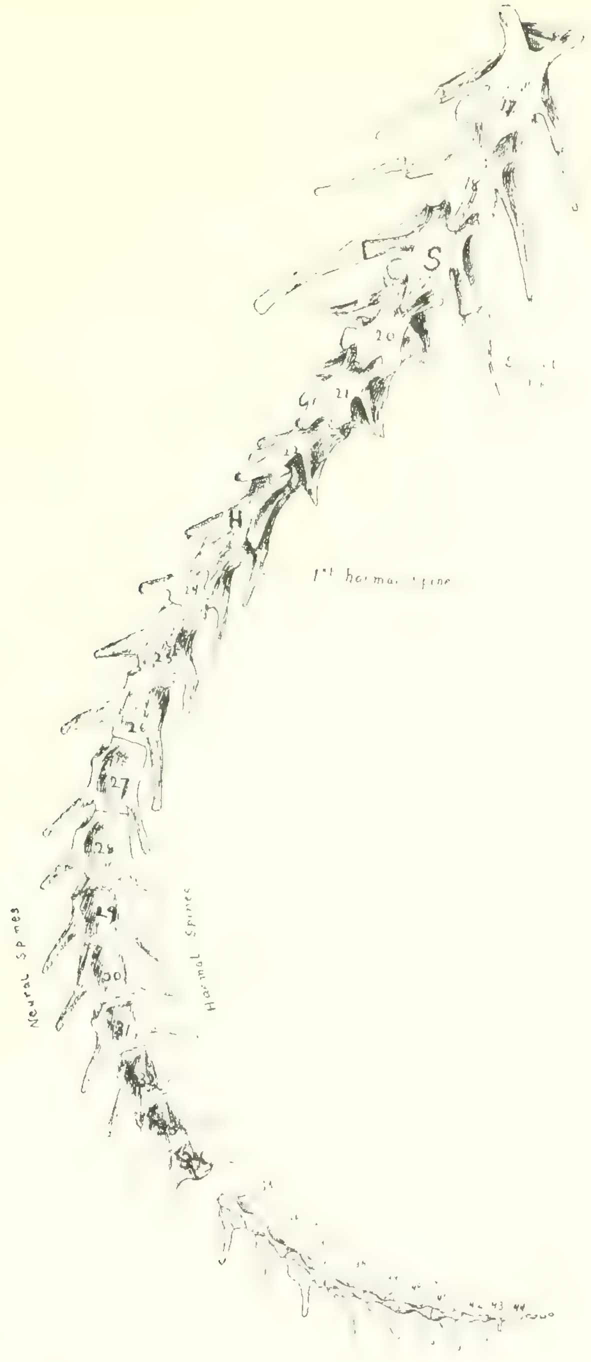
Fig. 19. Lower leg and pes—dorsal view of right.

PLATE 67

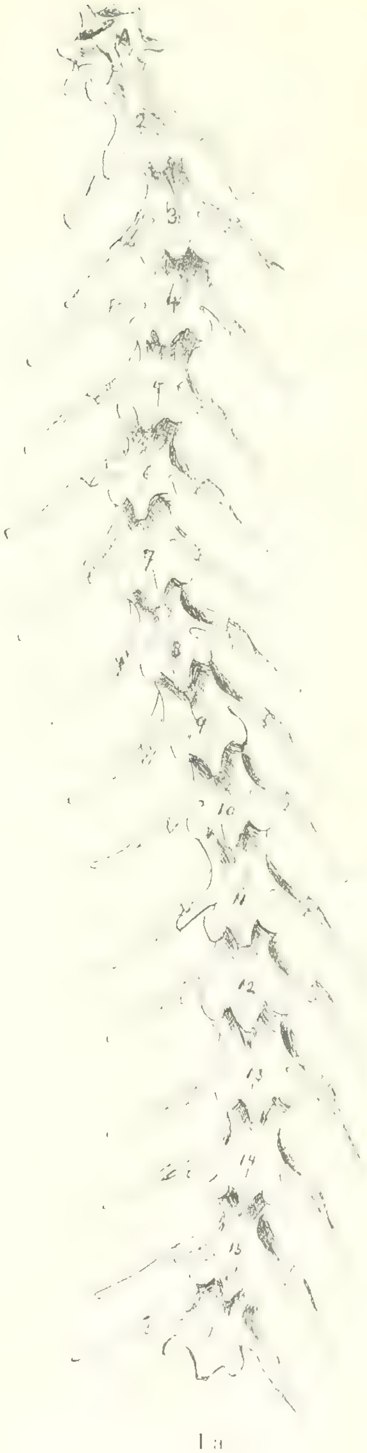
Fig. 20. Ventral view of pelvic girdle.

Fig. 21. Dorsal view of pelvic girdle.

Printed, January, 1903.



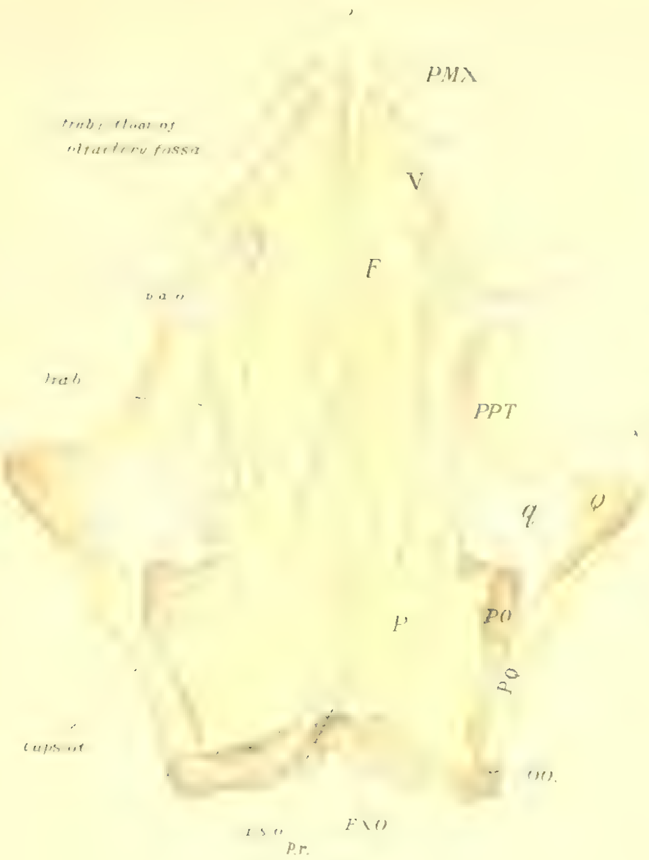
1 b

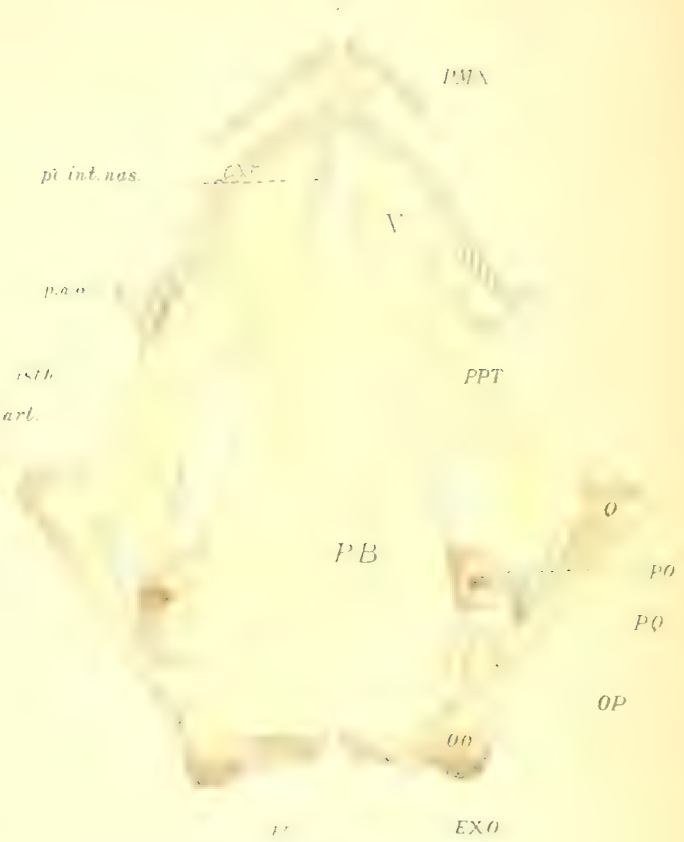


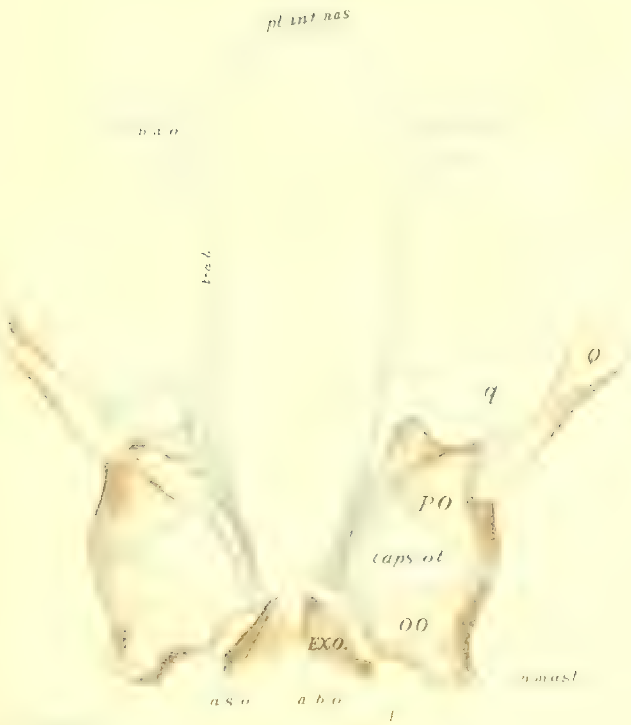
1 a

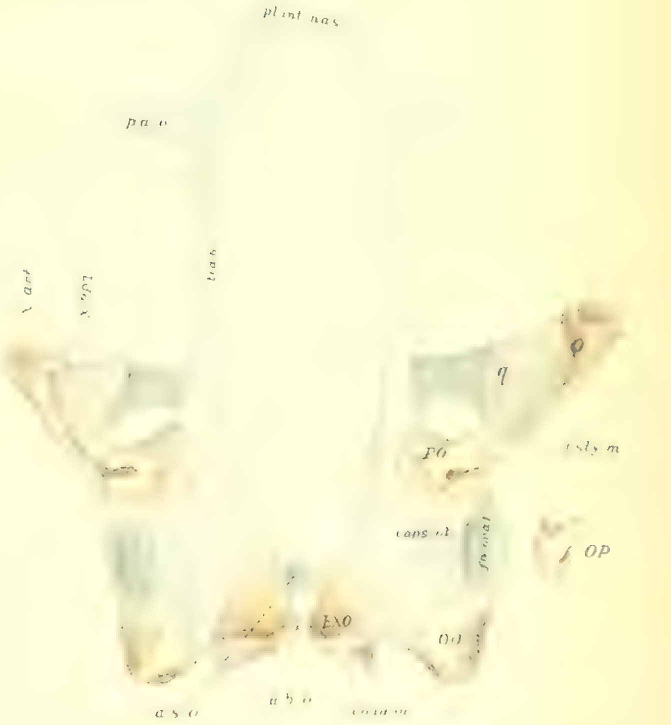
H. H. Wilder del.

WILDER: SKELETAL SYSTEM OF NECTURUS.

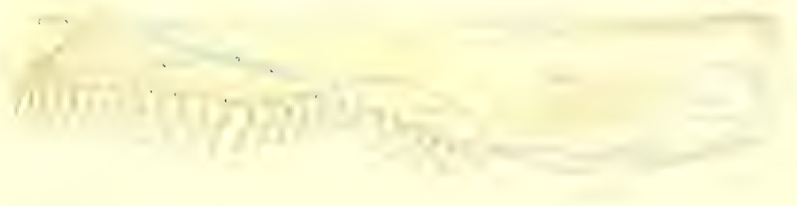

PMX
trab: floor of olfactory fossa
V
F
p.a.o
trab
PPT
q
Q
P
PO
PQ
caps ot
OO.
a.s.o
EXO
P.r.


PMX
pl int. nas.
V
p.a.o
isth
s art.
PPT
Q
PB
PO
PQ
OP
OO
EXO

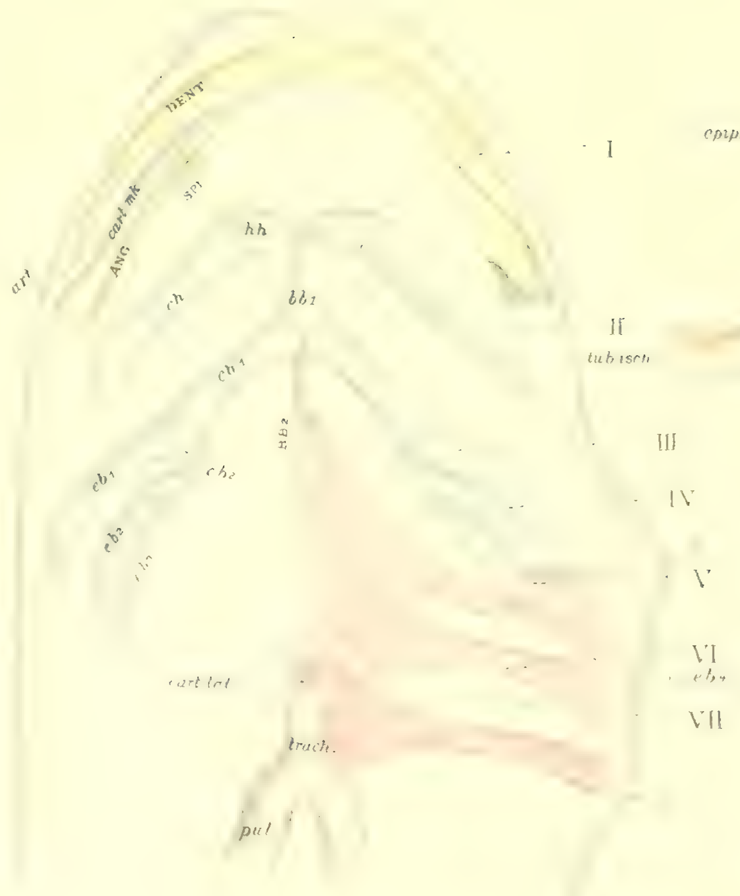

pl int nas
p.a.o
trab
Q
q
PO
caps ot
OO
EXO.
n mast
a.s.o
a.b.o

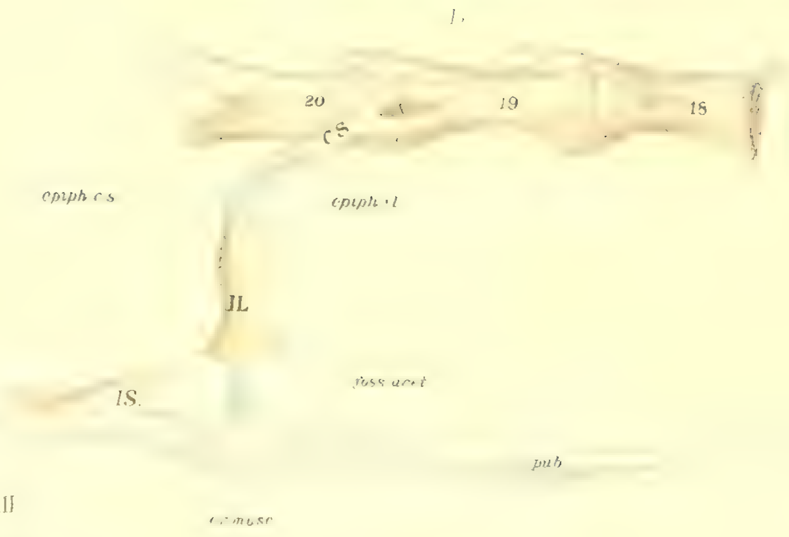

pl int nas
p.a.o
trab
s art
Q
q
styl m
PO
caps ot
OP
EXO
OO
a.s.o
a.b.o

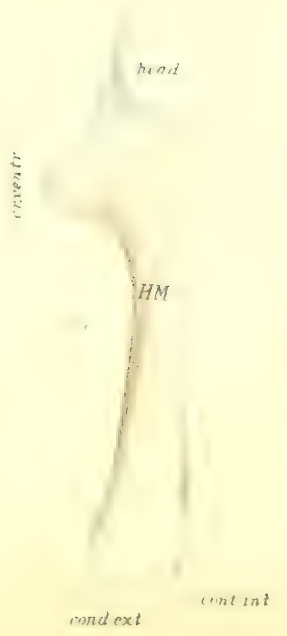
oo
Od
HA
Col
xix

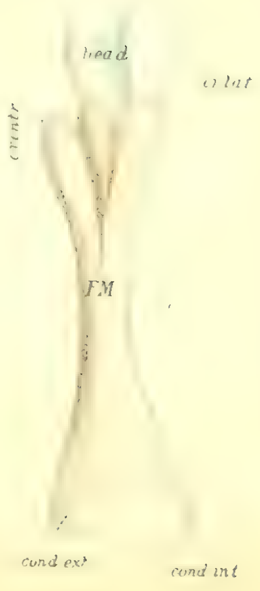


b
xix


DENT
cart mk
spl
ANG
art
hh
ch
bb1
cb1
bb2
cb1
cb2
cb2
I
II
tub isch
III
IV
V
VI
cb4
VII
cart lat
trach.
pul


1.
20
19
18
CS
epiph c s
epiph i l
IL
IS.
foss acet
pub
cr musc


head
cr ventr
HM
cond ext
cont int


head
cr lat
cr ventr
FM
cond ext
cond int

10. The Comparative Anatomy and Phylogeny of the Coniferales.

Part I.—The Genus Sequoia.[1]

By Edward C. Jeffrey.

(Read April 15, 1903.)

Introduction.

In the present and following memoirs, it is my intention to describe certain features of the anatomy of the Coniferales which appear to be of interest. The actual state of our knowledge of the morphology and history of the group is not sufficient to justify much certainty as to its classification, and consequently additions from any standpoint are likely to be of value. The prevailing views as to the relationship of the various orders of the Coniferales are based almost entirely on reproductive characters, and valuable as these must always be, they constitute, nevertheless, but a single line of evidence. The study of the anatomy of the older groups of Gymnosperms has done so much to clear up the question of their affinities that it does not seem unreasonable to expect that a good deal should be learned from investigations carried out on the same lines in the case of the Coniferales, the prevailing Gymnosperms of the present day. It is to be anticipated that the results of such investigations will serve to correct and supplement the conclusions drawn from the study of the reproductive organs alone.

The existing Sequoias are chosen as the subject of the first memoir, both because of their interest as the sole survivors of a genus which once flourished in many species throughout the entire northern hemisphere, and because investigations, already somewhat extensive although as yet incomplete, make it apparent that the genus Sequoia presents a striking example of those rare and important forms which so infrequently persist as links of transition between distinct and different natural orders of the present day.

The Stem of *Sequoia gigantea*.

Figure 1, plate 68, illustrates the structure of the wood in *Sequoia gigantea* as it appears in a transverse section of the heart of an old stem. There are three annual rings represented in the figure. In contrast to *S. sempervirens*, to be described later, the autumnal tracheids form a very narrow zone in each annual ring of growth, and the wood consequently lacks the strength which is characteristic of the latter species. The radial rows of tracheids are interrupted at intervals, especially in the autumnal region, by the resin cells which are so constant a feature of the wood of the *Taxodineae* and *Cupressineae*. As has been pointed out by Penhallow (Generic characters of North American *Taxaceae* and *Coniferae*, Proc. and trans. roy. soc. Canada, 1896, series 2, vol. 2, p. 33), the resin ducts, found so frequently in the wood of the *Abietineae*, are absent in the mature ligneous cylinder of *S. gigantea*. Figure 2, plate 68, gives a general view of the central cylinder of a branch of a young tree from the arboretum of Leland Stanford university, California. The stem is a year old and shows as a consequence a single ring of wood. The resin cells of the wood are poorly developed as yet, although those of the phloem are very apparent in spite of the comparatively low magnification. The minute structure of the fibrovascular tissues cannot be made out.

---

[1] Harvard Botanical Memoirs. — No. 7.

Figure 3, plate 68, is of the central cylinder of a five year old branch of *S. gigantea* taken from a tree which had already produced cones and seeds. The autumnal wood is relatively much thicker than in the old stem shown in figure 1. The feature of special interest in this section is the presence of *resin ducts* in the inner region of the *first* annual ring. Figure 4, plate 68, shows the first annual ring and the resin ducts more highly magnified from another section, cut from a different twig of the same main branch. As the material came from the Gray herbarium of Harvard university and was consequently in a dried condition, the cells surrounding the resin ducts show no evidence of the presence of protoplasm and a nucleus; but the obviously resinous contents of the ducts in the dry condition, as well as the parenchymatous nature of the cells surrounding them, leave no doubt as to their identity. In the last mentioned figure, the cells enclosing the lumen of the resin canals appear darker as to their walls than the adjacent tracheids. This is due to the fact that they become stained very intensely with haematoxylin, and thus are more non-actinic than the surrounding tracheids, counterstained less strongly with aqueous saffranin. The material presenting these peculiarities in the first annual ring was taken from specimens accompanied by unusually large cones, and labeled "J. G. Lemmon, California." In order to test whether the structures in question were not abnormalities, sections were made from two other lots of material from the Gray herbarium, marked "Bridges 331" and "Henry 1086," respectively. Figure 5, plate 68, shows the central portion of a transverse section from the material marked "Bridges 331." The resin ducts are obviously even better developed than they are in figure 3. Sections from the other lot of material also showed the presence of large and typical resin ducts in the *first* annual ring of the wood. The resin passages just described disappear in the upper part of the annual ring as it reaches what was originally the end of the yearly growth in length of the branch. In no case which has come under my observation did the resin ducts of the first year's growth in one annual segment of a branch become continuous with those in the next upper segment representing a subsequent year's growth in length. As a consequence the resin ducts of each first annual ring form a closed system and are confined entirely to their own segment of the branch. There are, further, no lateral anastomoses of the ducts in the same annual ring. In the weaker lateral twigs of the branches from the three lots of material mentioned above, resin ducts were generally found to be entirely absent. Through the kindness of Prof. C. V. Piper, I received formalose material of the branches of a young tree twenty years old, grown at Pullman, in the state of Washington. Not even the largest and most vigorous branches in this material showed any indication of the presence of resin ducts. Similar observations were made in the case of alcoholic specimens supplied to me by Dr. A. A. Lawson, of the Botanical department of Leland Stanford university. It may consequently be stated that so far as the present observations go, the presence of resin ducts in the first annual woody ring of *S. gigantea* is confined to the more vigorous branches of older trees which have already produced female cones, and that the phenomenon is normally absent in the smaller twigs of large trees as well as in the entire branch system of young trees.

THE REPRODUCTIVE AXIS OF *S. gigantea*.

In figure 6, plate 68, is seen the woody portion of the base of the female reproductive axis of *S. gigantea* in transverse section. In the first annual ring are numerous large resin ducts similar to those described above in the case of the more vigorous vegetative shoots of adult trees. The second annual ring is very broad and is quite free from resin passages. It is followed by a number of much narrower rings equally free from resin canals. The peduncular portion of the reproductive axis of *S. gigantea* continues to grow in thickness for some time after the seeds have been shed, and in this respect it resembles certain species of Pinus with persistent cones, and at the same time presents a marked contrast to *S. sempervirens*. Figure 7, plate 68, shows the center of the same section more highly magnified. The size and distribution of the resin ducts and of the resin cells also can be very well made out. Figure 8, plate 68, reproduces a cross section of a higher region of the same peduncle. The narrow annual ring containing the resin ducts seen in the last two figures, has disappeared, and the broad second ring of annual growth now abuts directly on the pith. In figure 9, plate 69, there is represented an intermediate region between those shown in figures 6, 7, and 8, of plate 68. Some of the resin canals in this section are very much enlarged. This appearance is due to the fact that the resin ducts end upwardly in resin pockets of considerable size. Figure 10, plate 69, illustrates the structure of the reproductive axis proper as seen in cross section at a height much above any of the foregoing. The resin ducts have reappeared in the wood close to the medulla, which in the present figure presents an elliptical outline due to the fact that two fructiferous scales of the cone derive their fibrovascular supply from the central cylinder of the axis in this region. The resin canals are particularly well developed around the bays corresponding to the departing traces of the fructiferous scales. The figure includes only part of the first annual ring of wood. In the reproductive axis of *S. gigantea* there are two annual rings of wood only, in the portion corresponding to the cone proper, and as a consequence growth does not continue after the second year when the seeds are ripe. The additional annual rings which are characteristic of the peduncle of the cone gradually die away in the transitional region between the peduncle and the axis proper. It is to be noted that there is no connection between the resin ducts of the peduncle and those of the proper axis of the cone, a condition quite similar to that described above for the successive longitudinal annual segments of the more vigorous vegetative branches of adult trees. I have not yet found any cone of *S. gigantea* in which the resin canals were absent from the first year's growth of the wood.

In figure 11, plate 69, is seen a transverse section through the woody portion of the base of a cone scale, including all of the first annual ring of growth and a narrow zone of the second. On the lower side of the first annual ring, resin ducts appear near the medulla. These form the direct continuation of the resin ducts of the axis shown in figure 10, plate 69. In figure 12, plate 69, is represented a section through a somewhat higher region of another fructiferous scale. In the center appears the medulla, above and below it is the wood of the fibrovascular system of the scale. The most interesting feature of this figure is the large number of resin canals present in the wood. Of these there are two series: the one composed of larger and less numerous ducts nearer the pith, and the other made up of smaller and more numerous ducts, farther out in the wood of the scale. Both series of ducts tend to become divided by radial partitions, and the two systems are not infrequently united by radial anastomoses as well, comparable to the radial canals running in the medullary rays of most of the *Abietineae*. The last two figures present extreme conditions in the modes of occurrence of resin canals in the wood of the fructiferous scales. Where the ducts are least abundant they are confined to the lower side of the scale as in figure 11, plate 69, and form a single series. They may also extend as a single series to the upper side of the scale. When the system of ducts is double, it may be double on the lower side of the scale only, or on one or other wing of the scale as well, or finally as in figure 12, plate 69, the double series may extend all around the medulla. Whenever a double system of ducts extends more or less completely around the wood of the scale, the series nearer the medulla is always complete, whatever may be the case with the more external series. The more complex arrangements of the resin canals just described are more often found in the upper scales of the cone. The outer system of ducts, unlike the inner one, never extends down into the axis of the cone, although it may pass far up in the bundles into which the fibrovascular tube of the base of the scale breaks above.

In figure 13, plate 69, is seen a transverse section of the upper broad portion of the fructiferous scale. The scale is covered on both the upper and the lower surfaces with a layer of periderm. In the fundamental tissue of the scale are numerous large resin passages as well as numerous sclerenchymatous cells. There are present two systems of fibrovascular bundles oriented in opposite directions, of which the upper series is less well developed and consists of somewhat smaller bundles. Along the upper margin of the lower set of bundles, which are the better developed, can be seen small, light dots which mark the position of intrafascicular resin ducts. These are continuous with those described above as occurring in the lower portion of the woody skeleton of the scale. Resin canals are much more commonly present in the lower series of bundles of the flattened upper part of the fructiferous scale than they are in the upper series, possibly on account of the greater robustness of the former. Figure 14, plate 69, shows a portion of the same section more highly magnified. The structure of the fundamental tissue can be more clearly seen. It consists of parenchymatous elements, of long sclerenchymatous elements present in cross section, and of large resin passages. Within the inner boundary of the woody tissue of most of the lower bundles can be seen one or more resin ducts. These are absent from the upper bundles. Figure 15, plate 69, represents another part of the same section. The fundamental tissue presents no difference from that shown in the preceding figure; but the bundles which belong to the lower series, towards the margin of the scale, are obviously united by strands of tissue running from their inner borders. The tissue in question is made up of transfusion cells. The smaller terminal bundles of the extreme upper portion of the fructiferous scale of *S. gigantea* are all more or less completely united at their inner borders by transfusion cells. The bundles likewise frequently terminate in transfusion tissue as well. Occasionally towards the lower part of the course of the bundles, as they become united into the fibrovascular tube of the base of the scale, the enormously developed transfusional borders of the bundles bend inwards and fuse more or less completely together, giving rise to a peculiar pseudomesarch type of bundle such as is shown in figure 16, plate 69. In this figure, two resin canals are to be seen in the secondary wood. Subtending the part of the secondary wood containing the two resin ducts, is a mass of parenchyma which is enclosed incompletely on the opposite side by wing-like extensions of the secondary xylem. These are in turn completely covered by a thick zone of very dense transfusion tissue. The phenomenon just described is not of very common occurrence and in all probability no very great morphological importance is to be attached to it.

THE SEEDLING OF *S. gigantea*.

Figure 17, plate 70, reproduces a transverse section of the woody portion of a five year old seedling of *S. gigantea*, collected by Prof. Asa Gray in the famous Calaveras grove of Big Trees, during his visit to California in 1872. I owe this duplicate specimen to the kindness of my colleague, Prof. B. L. Robinson, curator of the Gray herbarium. Four annual rings are shown in the figure. The resin cells which are so conspicuous in the wood of the adult stem are much less strikingly present in the seedling, and resin ducts are entirely absent even from the first annual ring. Through the kindness of Dr. Joseph L. Goodale, I have had the opportunity of examining several other seedlings of *S. gigantea*, grown on his estate at Ipswich. In none of these did I find any indication of the presence of resin canals in even the first annual ring of woody growth.

EFFECTS OF WOUNDS ON THE WOODY TISSUES OF *S. gigantea*.

Figure 18, plate 70, represents part of a transverse section of a wounded root of *S. gigantea*, in which the wounded area has become completely callused over. Towards the right in the figure, may be seen a mass of callus tissue. In the ring of growth just below the callus, is to be made out a long row of traumatic resin ducts stretching completely across the figure. The annual ring containing the resin canals, although axial to the callus, was formed subsequently to the wounding of the tissues, as was made out by examining the whole line of injury. The resin ducts are quite similar to those occurring normally in many of the *Abietineae*, and are generally surrounded by but a single layer of cells. Of these cells some are normal glandular cells, such as usually surround the lumen of resin canals where they occur in the wood of the *Abietineae*, while others are "resin cells," and are distinguished by their thick and strikingly pitted walls. In figure 19, plate 70, is represented part of the outer margin of the wood in a transverse section of the peduncular portion of the cone of *S. gigantea*. Very large resin canals appear along the inner border of the vernal wood in the last annual ring. These are surrounded by secretory cells; but as the figure was made from dry material the latter have almost completely collapsed. The formation of true resin canals in this case was due to the same cause as in the root just described above. I have seen a large number of instances of the formation of traumatic resin canals in the wood of both the root and the stem of *S. gigantea* and consequently am of the opinion that it is quite a usual result of injury. It should be added, however, that the formation of parenchymatous wood containing a large number of resin cells and ordinary parenchyma cells is even more commonly present in the case of wounds. This is especially the case with large exposed wounds on the aerial portions of the stem, where there is much necrosis and drying out of the woody tissue. In smaller wounds, however, where there is not too great an exposure of the ligneous cylinder to desiccation, the formation of the traumatic resin passages described above is very common. It should be noted finally that the traumatic resin canals of *S. gigantea* are formed in the vernal wood and in this respect are in contrast to those occurring in *S. sempervirens* under similar conditions, which, as will be shown later, make their appearance in the autumnal wood. I have found examples of the formation of resin canals in the phloem of *S. gigantea*, as well as in the wood, and as the result of a similar cause. I have discovered no instance of the occurrence of resin ducts in the fibrovascular cylinder of this species, except in the first year's growth of vigorous young branches of adult trees and in the axis of female cones (as described in earlier paragraphs), which could not be clearly traced to a previous injury. It seems extremely probable that the formation of traumatic resin canals in *S. gigantea* is to be regarded as a case of reversion to an ancestral condition, especially in view of the mode of occurrence of normal resin canals in certain instances as described above. The arguments in favor of this view, however, are best deferred to a later stage.

TRAUMATIC RESIN CANALS OF THE *Abietineae*.

It seems necessary in the meantime to refer preliminarily to certain other facts of a similar nature which have been made out in the case of the *Abietineae*, in a series of researches of which the present investigation forms a part. It has long been known that resin ducts are generally absent in the wood of the Abietineous genera, Abies, Tsuga, and Cedrus, and that they are replaced in many instances by resin cells. For the present the first-named genus will alone be considered; for as I hope to show subsequently, the other two genera resemble it very closely in the features which are of interest in this connection. *Abies firma* is described by Prantl (Engler u. Prantl, Nat. pflanzenfamilien, Coniferae, 1889, p. 37) as differing from the other species of Abies in normally possessing resin ducts in its wood. Penhallow (*op. cit.*) has more recently described the presence of resin canals, occurring in isolated annual rings of *Abies nobilis* and *Abies bracteata*. I have been able to confirm these observations in the beautiful series of sections of North American woods published a few years ago by Professor Penhallow. The resin ducts occur in long tangential rows in both the last-named species. I have myself examined a number of species of the genus Abies, and have found resin canals of very frequent occurrence under conditions to be more fully described on another occasion. For the present, however, it may be stated that resin ducts are extremely apt to be present in the female reproductive axis of various species of Abies, even when they are quite absent from the woody tissues of the ordinary vegetative stem. For example, in *Abies grandis*, according to Penhallow, there are no resin ducts present in the wood. Figure 20, plate 70, shows the general structure of the woody axis of the upper portion of the female cone of *A. grandis*. The specimen from which the figure was made, was secured at the Gray herbarium, and as a consequence the tissues have suffered a good deal from long desiccation. Nevertheless, indubitable resin ducts can be clearly made out in large numbers in practically the whole circumference of the woody cylinder of the cone. They are of quite the normal type and are surrounded by glandular cells which still retain the remains of their protoplasm. The section through the small upper end of the cone axis was chosen because it permitted of showing the structure of the *whole* of the ligneous portion of the tissues of the cone on a sufficient scale of magnification to make clear the presence and mode of distribution of the resin canals. In figure 21, plate 70, is seen a similar view of the woody tissues in the cone of *Abies balsamea*. This species is devoid of resin ducts not only in the wood of the vegetative axis but also in that of the cone. The figure in this case was made from material which had been properly preserved. Figure 22, plate 70, is made from a section through an injured root of a small tree of *Abies balsamea* growing in the Botanic garden of Harvard university. The figure includes all the xylem as well as a portion of the phloem of the injured root. There is an interruption of continuity in the latter tissue on the lower side, due to an incised wound which was made in all probability by a spade used in digging the soil about the tree. The woody tissue is likewise interrupted in the same region as the phloem, and on one side the last annual ring is separated for some distance from the tissues below. There is a considerable formation of resinous tissue along the inner margin of the last annual ring on both sides of the wound, which takes the form of resin cells. Farther away from the wounded portion, on the left, the resinous tissue gives place to a tangential row of resin ducts continuous through almost half the circumference of the root, and passing on the right into a narrow zone of resin cells, which are in turn continuous with the thick mass of resinous tissue on the immediate border of the wound. The center of the root is occupied by a resin duct surrounded by resinous cells, such as is commonly found in the axial wood of the root in the genus Abies (de Bary, Comp. anat., 1884). My investigations on this genus, although not yet complete, show that resin canals occur very frequently in the female reproductive axis, even when they are quite absent from the wood of the vegetative stem and from the root as well, except in the axial primary wood as just mentioned above. In all cases where I have been able to make the experiment, however, I have succeeded in bringing about the formation of resin canals as a result of injury, in the wood of species of Abies which are normally without them, even in their reproductive axis. It is interesting in this connection to note that certain fungous diseases causing injury to the wood of species of Abies produce the same result. It seems necessary to record the traumatic reactions of the woody tissues of the genus Abies because, as I shall attempt to show at the end of this essay, they supply an interpretation of the similar phenomena in the case of Sequoia.

The Leaf of *S. gigantea*.

In figure 23, plate 70, is seen part of a section through the base of the leaf of *S. gigantea*. In the center of the figure lies the leaf trace flanked by the two lateral wings of transfusion tissue, which are so characteristic of the lower part of the foliar bundle in Sequoia and its allies. Above and below the leaf trace are masses of collenchymatoid tissue. The feature of greatest interest in the figure is, that contrary to other described coniferous leaf traces, the foliar bundles of *S. gigantea* contain a resin duct. The duct is quite of the normal type and is surrounded by a single, almost complete row of resiniparous cells. In some cases, however, as is often found in the resin canals of the Sequoias, the parenchymatous lining of the canal is far from being continuous, and the tracheids as a result often abut directly on its lumen. It must not be supposed that resin ducts occur in all the leaf traces of *S. gigantea*, for this is not the case. They appear only to be present in the bundles of the very large leaves of exceptionally vigorous branches of mature trees (*i. e.*, trees which have already ripened seed). All the material which I have, showing this feature, came from the Gray herbarium of Harvard university; but in spite of the necessarily bad condition of preservation consequent on its origin, there seems to be no reasonable doubt as to the nature of the canals, which I have described above as resin ducts. The longitudinal range of the resin ducts of the foliar bundles of the largest leaves in mature trees of *Sequoia gigantea* is quite limited; for they appear only after the leaf trace has passed quite out into the cortex of the branch, and indeed after it has traversed a considerable part of its upward and outward course. There is as a consequence no communication between the resin ducts of the first annual ring of wood in the branches and those appearing in the leaf traces. Like the other modes of occurrence of resin canals described above, there is an entire absence of correlation with other similar tissues. The resin ducts of the leaves disappear again very shortly after the leaves have emerged from the surface of the branches, so, as has just been stated above, the longitudinal course of the resin canals of the leaf traces, where they occur, is very short indeed.

THE STEM OF *Sequoia sempervirens*.

Penhallow (*op. cit.*) has noticed the occurrence of continuous tangential rows of what he terms "imperfect resin ducts" in the wood of the old stem of *S. sempervirens*. The phenomenon seems to be extremely rare, for I have found very few examples although a large number of different specimens of the wood of this species has been examined in this connection. Professor Penhallow has been so kind as to send me a very good example illustrating this peculiarity, and as it is much more striking than any other I have seen, all the accompanying figures of the mature wood of *S. sempervirens* are made from this material. In figure 24, plate 70, a part of a transverse section of the wood of *S. sempervirens* is represented under a low magnification. There are four annual rings present in the figure. Mingled with the tracheids in all the four woody rings are numerous resin cells, such as have been described above in *S. gigantea*, and such as occur commonly in the other *Taxodineae*. The autumnal wood in *S. sempervirens* forms a much thicker zone than in *S. gigantea*, which is the cause of the greater weight and strength of the wood in the former species. In the second annual ring from the top of the figure are to be seen the resin ducts first described for *S. sempervirens* by Penhallow (*op. cit.*, p. 39, pl. 6, fig. 2). They are obviously situated in the autumnal wood and in this respect present a marked contrast to those of *S. gigantea* described in the foregoing paragraphs, for in the latter species they occur in the vernal portion of the annual ring. In their distribution the resin canals in the present instance resemble those formed as the result of injury in *S. gigantea*, species of Abies, *etc.*, and form a continuous tangential zone, such as is characteristic of traumatic resin canals. Figure 25, plate 71, shows a portion of the annual ring containing resin ducts more highly magnified. There is obviously a sharp transition from the autumn wood to that of the following spring in the size of the tracheids and the thickness of their walls. There are numerous resin cells on the outer margin of the autumnal wood. Farther inwards, the autumnal tracheids give place to parenchyma cells, which, on account of the fact that the material is from the heart wood of an old tree, are quite devoid of protoplasmic contents. They are unmistakable, however, since their walls are composed of cellulose and stain a deep blue with haematoxylin. About the lumina of the resin ducts, the parenchymatous cells are as a rule strongly pitted and closely resemble the resin cells of the medullary rays in certain Conifers.

In figure 26, plate 71, is shown a transverse section of a young branch of *S. sempervirens* from material sent to me by Dr. A. A. Lawson of the Botanical department of Leland Stanford university. The bases of four leaves clearly appear on the margin of the figure. These originate from the branch by a flat base in contrast to the rounded mode of origin found in *S. gigantea.* In two of the leaves there are obviously three resin canals in the mesophyll, another point of contrast to *S. gigantea* and most of the other *Taxodineae* and *Cupressineae*, where there is as a rule but a single resin duct in the parenchyma of the leaf, and immediately under the fibrovascular bundle. The material from which the illustration has been made was cut and preserved in California on the 2d of May. The growth of the present year's ring of wood has begun and has already reached a considerable thickness. Branches of *S. gigantea* cut from trees at the same spot and at the same time show scarcely any signs of the commencement of cambial activity. The slowness of initiation of cambial activity in the Big Tree is no doubt one, at least, of the causes of its greater hardiness. There are no resin ducts to be seen in the wood of the young branch, appearing in transverse section in the figure, and in this respect the illustration might stand for any branch of *S. sempervirens*; for I have not found even in the most robust ramifications of the mature trees of this species any indication of the resin canals, which are so often present in the first annual woody ring of *S. gigantea.*

TRAUMATIC RESIN DUCTS IN *S. sempervirens.*

In some of the specimens sent me by Dr. Lawson from the arboretum of Leland Stanford university the phenomenon of fasciation was present. As this feature of *S. sempervirens* has recently been fully described by Pierce (Studies on the Coast Redwood, Cal. acad. sci., 1901), it will not be necessary to refer to it here. The wood in most of the fasciated specimens was quite normal as regards the absence of resin canals; but in the subterranean portion of a dead branch which had taken on the flattened mode of growth so characteristic of fasciation, numerous resin ducts were found in tangential rows. The shoot in question had obviously been injured and the appearance of resin canals is doubtless to be correlated with the diseased condition of the tissues. Figure 27, plate 71, is made from a section through this branch. There are two annual rings present and it is in the first of these that the resin ducts are to be seen. The ducts are in tangential rows and are situated in the autumnal wood just as in figure 25, plate 71. In figure 28, plate 71, are represented some resin canals from another section of the same material, highly magnified. The resin ducts are obviously surrounded for the most part by cells still containing protoplasm and a nucleus, although in some cases the tracheids abut directly on the lumen of the resin canal. The structure of the ducts shown in the figure is quite typical of the resin passages I have found in the Sequoias in general. It is a fact of considerable interest in the present connection, that the resin ducts first described by Penhallow for the wood of the old stem of *S. sempervirens* occur in the same tangential rows which are found in the obviously injured stem of the species under discussion, and under similar circumstances in the *Abietineae* as well. It is often the case that traumatic resin canals extend far above and below the actual spot of injury and it accordingly seems extremely probable that the rows of imperfect resin canals found in the otherwise quite normal fragments of wood of *S. sempervirens* are really due to an injury above or below the region from which the pieces of wood have been taken.

THE REPRODUCTIVE AXIS OF *S. sempervirens*.

In figure 29, plate 71, is represented the fibrovascular cylinder of the lower third of the reproductive axis of *S. sempervirens*. Although the cone from which the section was made had long shed its seeds, and had assumed an almost black hue from long exposure to the weather, there are obviously no indications of annual rings in the photograph. While the absence of annual rings does not absolutely prove that there are no additions to the secondary wood of the reproductive axis after the first year, still it appears very probable from the state of affairs in the cones of the other living species of Sequoia that such is the case. This view of the matter is further strengthened by the occurrence of perfectly normal annual rings in the vegetative organs of *S. sempervirens*. The question can, however, only be finally settled by the study of the growth of cones in the field. There are no annual rings in the peduncular portion of the cone of the species under consideration and in this respect it also presents a contrast to *S. gigantea*, where, as has been described above, there are numerous annual rings in that region of the reproductive axis. Further, resin ducts are entirely absent from all parts of the wood of the cone of *S. sempervirens*. Figure 30, plate 71, shows the structure of a cross section through the base of a cone scale of this species. The dense wood of the tubular central cylinder of this portion of the fructiferous scale shows no evidence of the presence either of the annual rings or of resin ducts, which are such notable features of the cone scales of *S. gigantea*. The specimen shown in figure 30 is quite typical in these respects; for I have examined a number of cones from different sources, without finding any examples of the occurrence of either of these structures. In figure 31, plate 71, appears a portion of a transverse section of the upper third of the cone scale of *S. sempervirens*. The large bundles along the lower side of the figure belong to the lower series. They are very much larger than those near the upper surface of the scale and are inversely oriented.

In the species under consideration there is a very much greater relative reduction of the upper series of bundles than is the case in *S. gigantea*. The commissures of transfusion tissue, which are so marked, especially in the lower bundles of the cone scales of the latter species, are much less well developed in the Redwood. The fibrovascular bundles of the fructiferous scales of *S. sempervirens* show no annual increments of growth and never contain resin ducts.

THE ROOT OF THE SEQUOIAS.

Figure 32, plate 71, illustrates the structure of a small root in *S. gigantea*. It is obviously pentarchous in its organization and very much resembles a root of *Pinus strobus* or some other Abietineous species with large polyarch roots. The protoxylem groups, however, which occupy the apices of the five rays of the primary wood, differ from those of species of Pinus, *etc.*, in not embracing resin ducts. Although the roots of the species under consideration are generally pentarchous, examples are not infrequently found in which there are only four rays of primary wood. This state of affairs also occurs in *Pinus strobus*. The primary root of all seedlings of *S. gigantea* which I have examined is of the tetrarchous type. I have never found resin canals present in the secondary wood of this species except as the result of injury.

The root of *S. sempervirens* is so similar to that of *S. gigantea* as scarcely to merit a separate description. The symmetry of the root is, however, almost always tetrarchous and the various histological elements are somewhat larger than in the latter species.

CONCLUSIONS.

In the foregoing paragraphs, attention has been called to the occurrence of resin ducts, under certain definite conditions, in the wood of Sequoia. In *S. gigantea*, which in all probability is the more primitive of the two surviving species, resin canals are constantly present in the wood of the peduncle, of the axis, and of the scales of the female cone. They also frequently occur in the first annual ring of the more vigorous branches of adult trees. Resin ducts likewise are sometimes found in the leaf traces of the larger leaves of well nourished, mature individuals. Finally, it is possible to bring about the formation of resin canals in tangential rows as the result of injury to the woody cylinder of the root stem and cone of *S. gigantea*. The resin ducts occurring in the various situations cited above, form entirely separate systems which do not communicate in any way with each other. In *S. sempervirens*, in contrast to the species just referred to, there are no resin canals in the woody tissues either of the reproductive organs, or of young branches, or even of vigorous leaf traces. In *S. sempervirens*, resin ducts appear only as tangential rows in isolated annual rings, probably in all cases in response to injury to the tissues of the wood.

The occurrence of resin canals in the reproductive axis of *S. gigantea* is in all probability to be regarded as an ancestral feature. It is significant in this connection that certain species of Abies, which have no resin ducts in the wood of their vegetative organs, retain them in the ligneous cylinder of their cones, *e. g.*, *A. grandis*, *A. nobilis*, *etc.*, *etc.* In the case of these species the presence of resin ducts as a general feature of structure of the wood in the order to which they belong, justifies the conclusion that the occurrence of resin canals in the wood of the female reproductive axis is an ancestral character, which has disappeared in the wood of the vegetative stem. A parallel case is presented by the peculiar mesarch bundles found by Dr. Scott in the peduncle of the cones in certain Cycads (The anatomical characters presented by the peduncle of *Cycadaceae*, Ann. bot., 1897, vol. 11). Bundles of this nature were present in the medullary crown of the vegetative axis of certain of the primitive fossil Gymnosperms and of the Cycadofilices. In the living Cycads, mesarch bundles have disappeared in the vegetative stem, but are sometimes retained in the reproductive axis and quite generally in the vegetative and reproductive leaves. In *S. gigantea*, resin ducts retained in the wood of parts of the female cones, likewise occasionally occur in the leaf traces as well, thus presenting a striking parallel to the mesarch bundles of the Cycads, in the manner of their distribution. The presence of resin canals under certain quite definite conditions in the first annual ring of the branches of *S. gigantea*, supplies a further argument for regarding the occurrence of resin ducts in the wood of this species as the retention of an ancestral feature, for it is only natural to find such a character reappearing in the *first* zone of woody growth of the young branch. This conclusion is also confirmed by the presence of a similar feature in the young branches of certain Abietineous species to be subsequently described.

The phenomena of injury furnish additional evidence in favor of the view that the ancestral stock from which the Sequoias have been derived, was characterized by the presence of ligneous resin ducts, for it appears justifiable to regard the formation of tangential rows of traumatic resin canals in the injured wood of both living species of Sequoia as a reversion to an ancestral condition, especially in view of the phenomena described in the last paragraph. This explanation of the phenomena resulting from injuries to the woody tissues in the species under discussion is confirmed by the fact that similar traumatic resin ducts are commonly formed as the result of injury to the wood in the *Abietineae*, in contrast to the *Cupressineae*, *etc.*

The hypothesis that the Sequoias have come from ancestors characterized by the presence of resin ducts in their woody tissues, receives a further support from the consideration of the anatomical structure of certain fossil species of Sequoia. Penhallow has described the presence of resin canals in the wood of *S. langsdorfii* (Notes on the Cretaceous and Tertiary plants of Canada, Proc. and trans. roy. soc. Canada, 1902, series 2, vol. 2, p. 44–45). The wood of this species, known heretofore only by its foliage and its fruit, is described as having occasionally imperfect resin ducts in its autumnal wood. Unfortunately the author does not figure nor further describe the distribution of the resin ducts in question, so it is not possible to have an opinion as to whether they were of traumatic or of normal origin. The resin canals in the case of *S. langsdorfii* had a longitudinal course in the wood. Quite recently, Professor Penhallow has announced the occurrence of radial resin canals in the wood of another species of Sequoia; but as yet no published account has appeared.

It seems highly probable, if the various arguments advanced above are valid, that the Sequoias have come from a stock characterized by wood penetrated by resin canals. If this probability be granted, the question immediately arises, whether they have come off from the same stock as the *Abietineae*, which have as a striking anatomical peculiarity the presence of resin canals in their ligneous tissues. At first sight this would appear to be an unlikely hypothesis; for the *Abietineae* are generally regarded (*cf.* Potonie, Pflanzenpalaeontologie, 1899, p. 322; Coulter and Chamberlain, Morphology of Spermatophytes, 1901, p. 108; Strasburger, Coniferen und Gnetaceen, 1872, p. 265; *etc.*) as a very modern order of the Coniferales. The reasons for this view are, however, not entirely apparent, for the genera Pinus and Cedrus appear in the infra-Cretaceous, and are thus as far as the palaeontological record at present goes, synchronous in their first appearance with Sequoia (R. Zeiller, Palaeobotanique, 1900, pp. 271 and 277). Further, so competent a judge as Dr. Scott states that "on the whole, it is impossible in the present state of our knowledge, to say which tribe or family of the Coniferae is the most ancient" (Studies in fossil botany, 1900, p. 483).

Much importance is justly attached to the structure of the female cone in the classification of the Coniferales, and any hypothesis of the phylogeny of the group must accordingly harmonize with the facts gathered from this source, *when properly interpreted.* In the *Abietineae*, the female cone is made up of double superposed scales. The most generally accepted explanation of the morphological nature of each pair of superposed scales is that the upper ovule-bearing scale represents the fusion of a pair of leaves, belonging to a reduced axis, axillary to the lower subtending bract (for an admirable account of this difficult question, see Worsdell, Structure of the female "flower" in the Coniferae, Ann. bot., 1900, vol. 14). This hypothesis finds a strong support from the standpoint of comparative anatomy, and as has recently been aptly stated by Professor Coulter, the clear and parallel case of reduction of an axillary (vegetative) shoot in

Sciadopitys is almost a demonstration of its accuracy. The hypothesis which explains the ovuliferous scale of the *Abietineae* as a reduced and modified short shoot (brachyblast), is likewise in harmony with teratological evidence, for in the so called proliferous cones of certain *Abietineae*, the ovuliferous scale becomes more or less completely transformed into a leafy bud and the subtending bract into an ordinary vegetative leaf. It is a curious and interesting fact, which does not seem to have been properly considered in regard to its bearing on the phylogeny of the Coniferales, that cases of proliferous female cones are confined, in the present state of our knowledge, to the *Abietineae* and the *Taxodineae* (Penzig, Pflanzenteratologie, 1894, vol. 2, p. 485–514). To those who accept the brachyblastic theory of the nature of the ovuliferous apparatus in the Coniferales, this state of affairs must appear weighty evidence in favor of the view that the *Abietineae*, and the *Taxodineae* as well, are somewhat primitive orders of the group, for there would naturally be the greatest tendency to reversion and the clearest anatomical evidence of the shoot value of the ovuliferous scale in the orders which are nearest to the ancestral stock.

In the case of the *Taxodineae*, the scales of the female cone are not superposed in pairs but consist of single, generally more or less thickened ovule-bearing organs, in which there is present a *double* system of bundles consisting of an upper and a lower series oriented in opposite directions, as are those of the separate superposed scales of the *Abietineae*. The generally accepted description of the state of affairs in the cone scales of the *Taxodineae*, is that there is a fusion of the ovuliferous and sterile bracts. It is scarcely logical to speak of organs as being "fused" unless they were originally separate. The view that they were primitively separate, superposed scales in the ancestral stock of the *Taxodineae* is strengthened by a consideration of the anatomical facts in the case of the genus Sequoia; for it is not easy to conceive that the series of massive bundles near the upper surface of the cone scale in this genus is arising *de novo* for the benefit of the reproductive organs, since the ovular bundles are extremely small and quite out of all proportion to the fibrovascular strands of the upper system from which they take their origin. The more reasonable explanation seems to be that the thick, single scale which bears the ovules in the case of most of the *Taxodineae*, is made up of a fusion of two separate scales which existed in a more primitive group, probably the *Abietineae* or their parent stock. This view of the matter receives further support from the peculiar manner of the occurrence of resin ducts in the woody tissues of living and fossil Sequoias.

It would be anticipating unduly the results to be recorded in subsequent memoirs on the Coniferales, to express more than a provisional opinion as to the position of the genus Sequoia but this much may be safely stated. The anatomy of living and fossil species of Sequoia goes to show that the genus has come from a stock possessing ligneous resin ducts, such as prevail in the *Abietineae* of the present day. It may be urged that this in itself is a very small point. Reply may be made that the mesarch structure of the primary woody bundles of the more primitive Gymnosperms and the adhesion of the stamens to the calyx in the *Rosaceae* are likewise small points, yet no well informed botanist doubts that they are important taxonomic criteria. It appears to be rather the significance than the magnitude of anatomical or morphological features which makes them of classificatory value. The peculiar and apparently most significant mode of occurrence of resin canals in the wood of the Sequoias points to their derivation from an Abietineous stock, which may of course have been ancestral not only to the Sequoias but also to the living genera of the *Abietineae* as well. This conclusion appears to be supported by a consideration of the structure of the female cone in the *Abietineae*, *Taxodineae*, and the Coniferales in general. Finally the derivation of the Sequoias from an Abietineous source is in no way contradictory to the palaeontological record.

SUMMARY.

1. Typical resin ducts occur in the wood of the peduncle, axis, and scales of the female cone of *Sequoia gigantea*.

2. Resin ducts are likewise present in the first annual ring of vigorous branches of adult trees of the same species. Resin ducts are normally absent in all the branches of immature trees.

3. Resin ducts are also found in the leaf traces of very vigorous leaves of adult trees of *Sequoia gigantea*.

4. Resin ducts are entirely absent from the wood of all parts of the cones of *Sequoia sempervirens*.

5. The same statement holds true of the branches and leaves of this species.

6. Resin ducts appear in tangential rows in the wood of root and shoot in both *Sequoia gigantea* and *Sequoia sempervirens* as a result of injury to the tissues.

7. A consideration of the mode of occurrence of resin ducts in the Sequoias leads to the conclusion that they are an ancestral feature of structure in the wood.

8. The anatomy of the vegetative organs and floral organs of the living Sequoias points strongly to their derivation from an Abietineous stock. This conclusion receives confirmation from what is known of the anatomy of the fossils, and finally is not in contradiction to the palaeontological record.

For help in securing the material for the present investigation, I wish to offer my best thanks to Miss Alice Eastwood, Sir William Thiselton-Dyer, Dr. A. A. Lawson,

Dr. D. H. Scott, Prof. D. P. Penhallow, Prof. C. V. Piper, Professors Farlow, Goodale, Robinson, and Thaxter, and last but not least, to Mr. George S. Shaw, chairman of the visiting committee on botany.

BOTANICAL MUSEUM OF HARVARD UNIVERSITY,
Cambridge, Mass.

EXPLANATION OF PLATES.

All the figures are from photomicrographs.

PLATE 68.

Fig. 1. Transverse section of the wood of *Sequoia gigantea*. × 50.
Fig. 2. Transverse section of a branch of a young tree of *S. gigantea*. × 60.
Fig. 3. Transverse section of a vigorous branch of an adult tree of *S. gigantea*. × 40.
Fig. 4. Transverse section of the medullary region of a similar branch. × 100.
Fig. 5. Medullary region of a similar branch from another adult tree of *S. gigantea*. × 50.
Fig. 6. Transverse section of the woody portion of the peduncle of an old cone of *S. gigantea*. × 30.
Fig. 7. Transverse section of the central portion of the same. × 50.
Fig. 8. Higher region of the peduncle of the same cone. × 30.

PLATE 69.

Fig. 9. Transverse section of the medullary region between those shown in figures 6 and 8. × 50.
Fig. 10. Transverse section through the axis of the cone of *S. gigantea*. × 40.
Fig. 11. Transverse section of the woody axis of the base of a cone scale in *S. gigantea*. × 50.
Fig. 12. Transverse section of the woody axis of another cone scale of *S. gigantea*. × 50.
Fig. 13. Transverse section through the upper portion of a cone scale of *S. gigantea*. × 3.
Fig. 14. Transverse section of part of the same. × 50.
Fig. 15. Transverse section of another part of the same. × 50.
Fig. 16. Transverse section through an abnormal bundle of the cone scale of *S. gigantea*. × 60.

PLATE 70.

Fig. 17. Transverse section of the woody part of the axis in a five year old seedling of *S. gigantea*. × 40.

Fig. 18. Transverse section through part of an injured root of *S. gigantea*, showing the formation of traumatic resin ducts in a tangential row. × 40.

Fig. 19. Transverse section through part of the peduncle of a wounded cone of *S. gigantea*. × 50.

Fig. 20. Transverse section of the upper portion of the woody axis of a female cone of *Abies grandis*, showing the presence of resin canals. × 40.

Fig. 21. Transverse section through the woody axis of the cone of *Abies balsamea*, showing the absence of resin ducts. × 35.

Fig. 22. Transverse section through the central portion of a wounded root of *Abies balsamea*, showing the presence of a tangential row of traumatic resin ducts. × 32.

Fig. 23. Transverse section through a leaf trace of a vigorous leaf of a mature tree of *S. gigantea* × 200.

Fig. 24. Transverse section of the wood of *S. sempervirens*, showing the presence of a tangential row of resin ducts. × 35.

PLATE 71.

Fig. 25. Part of the last section more highly magnified, showing the structure of the wood and the resin ducts. × 100.

Fig. 26. Transverse section of a young branch from an immature tree of *S. sempervirens*. × 30.

Fig. 27. Transverse section of part of an injured stem of *S. sempervirens*, showing the presence of tangential rows of traumatic resin ducts in the autumnal wood. × 50.

Fig. 28. Transverse section of another similar specimen, showing details of the structure of the traumatic resin ducts. × 200.

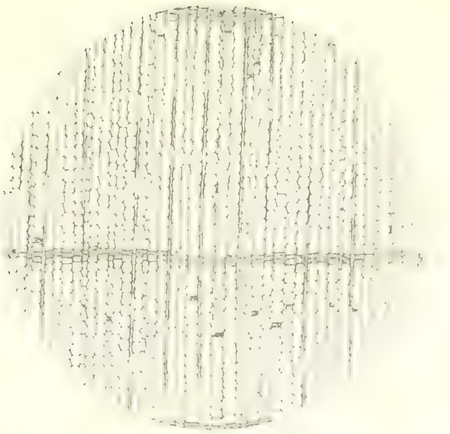
Fig. 29. Transverse section through the woody axis of the cone of *S. sempervirens*. × 35.

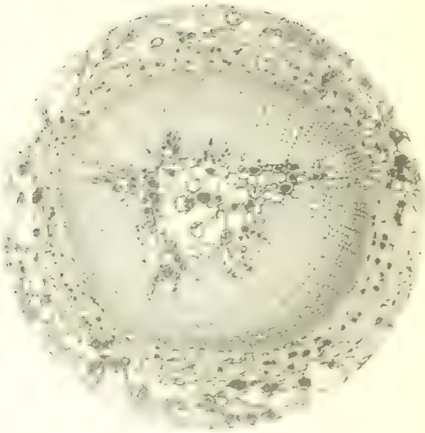
Fig. 30. Transverse section through the woody portion of the base of the cone scale of the same species. × 50.

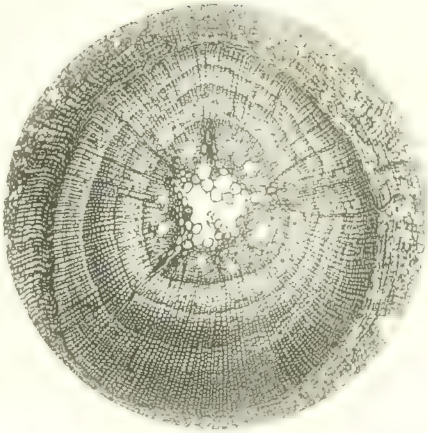
Fig. 31. Transverse section through the upper portion of the cone scale of *S. sempervirens*. × 40.

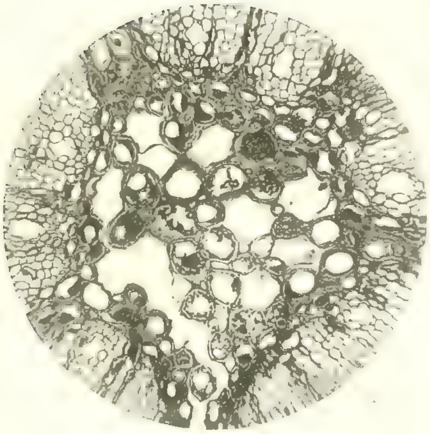
Fig. 32. Transverse section through the root of *S. gigantea*. × 40.

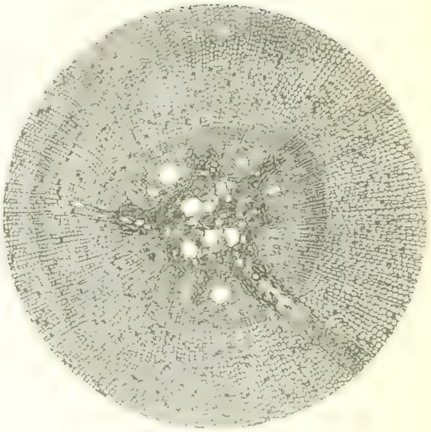
Printed, November, 1903.

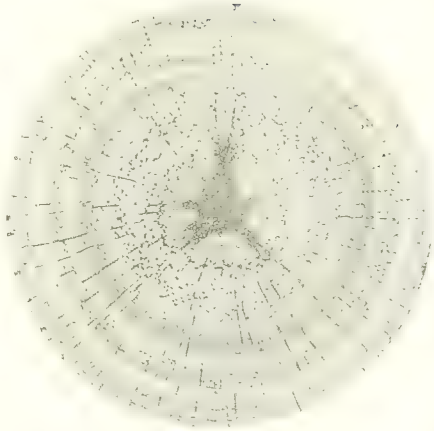


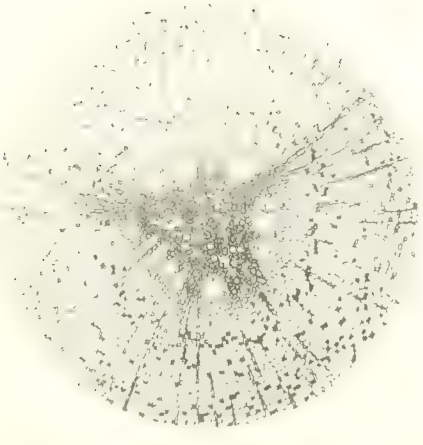


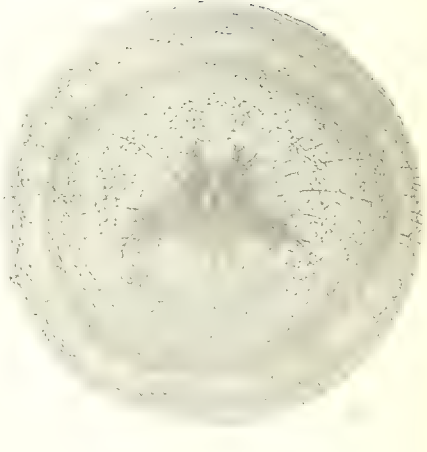


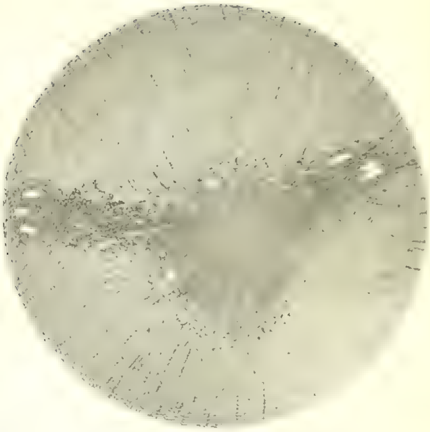


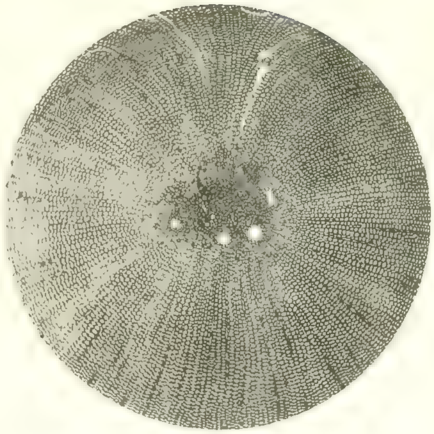


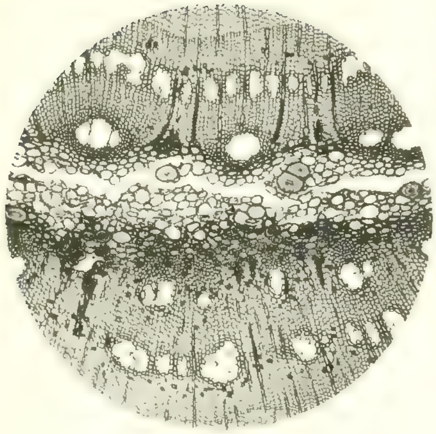


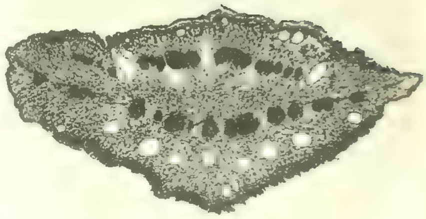


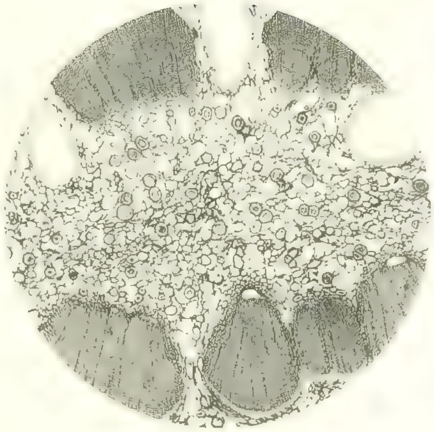


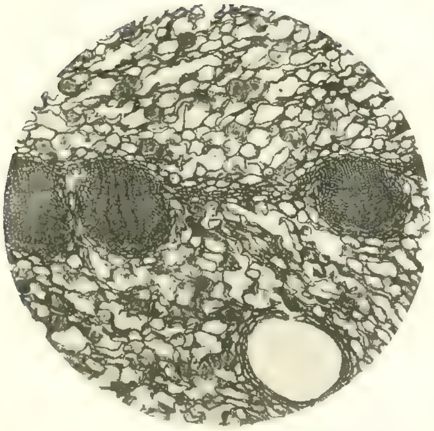


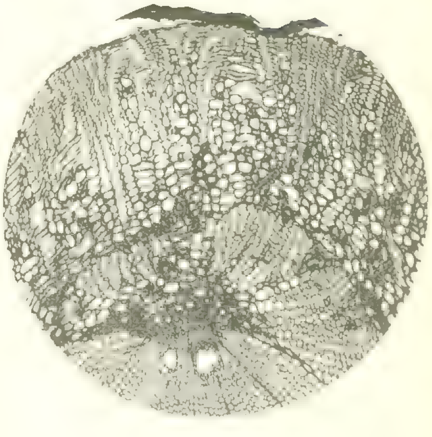


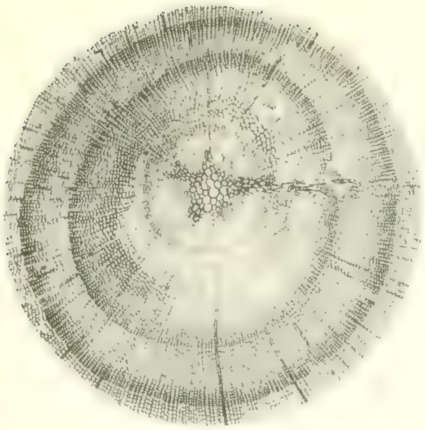


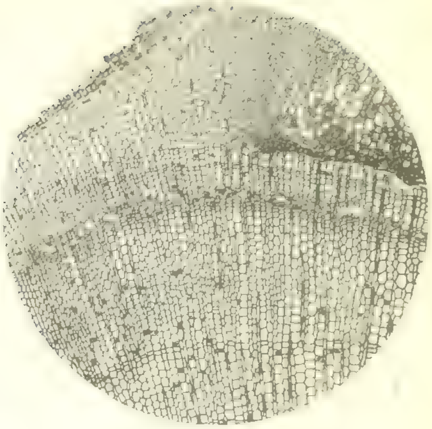


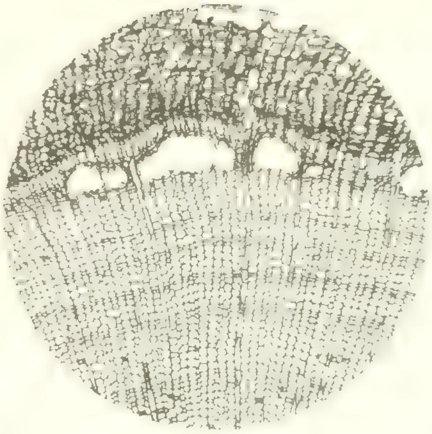


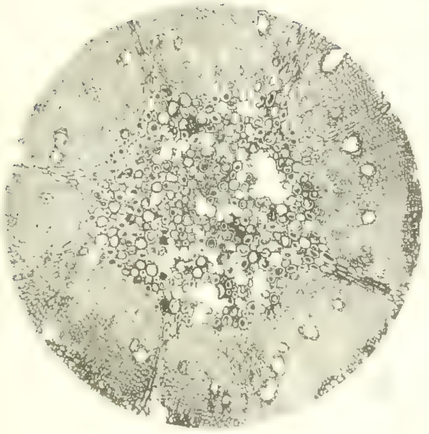


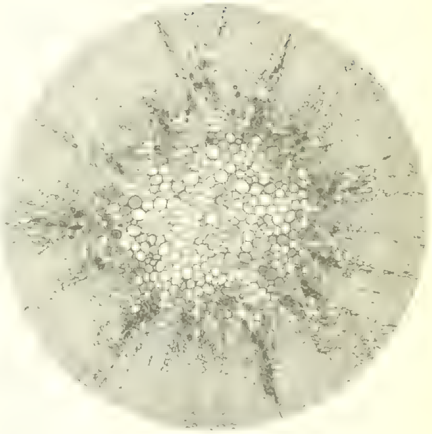


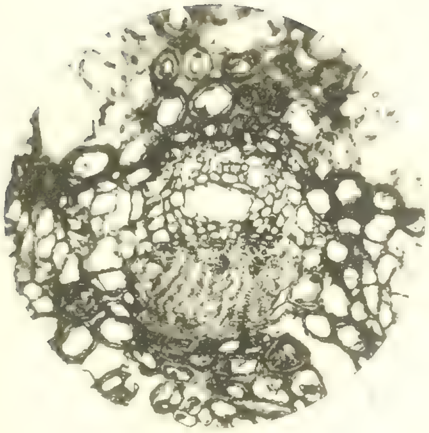


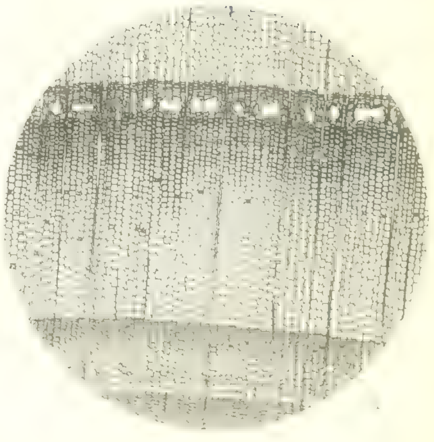


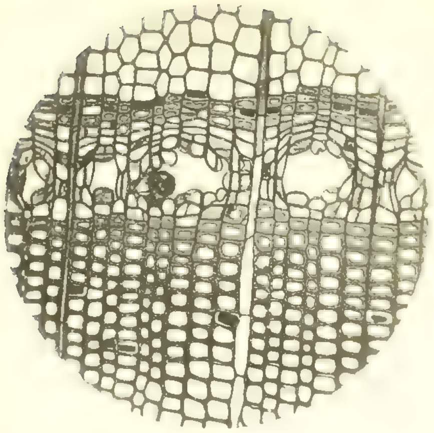


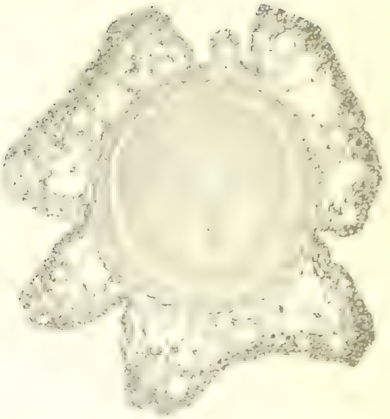


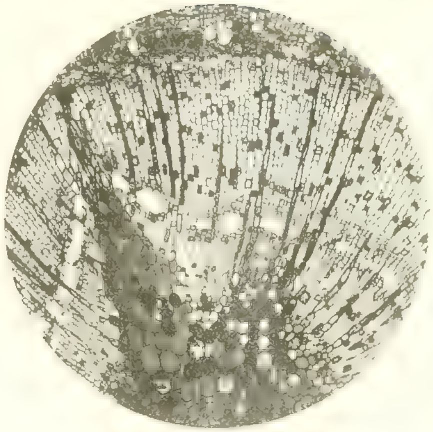


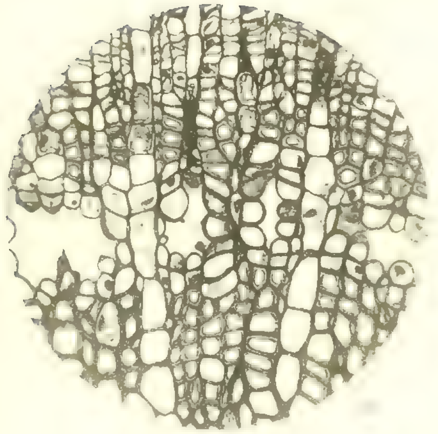


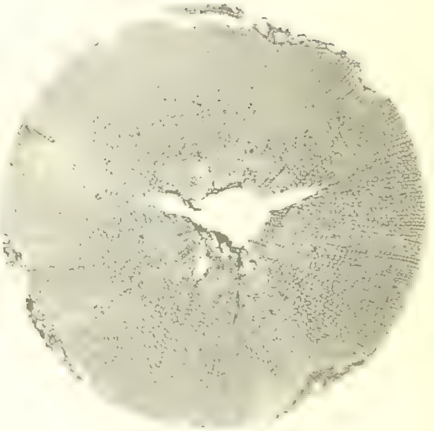


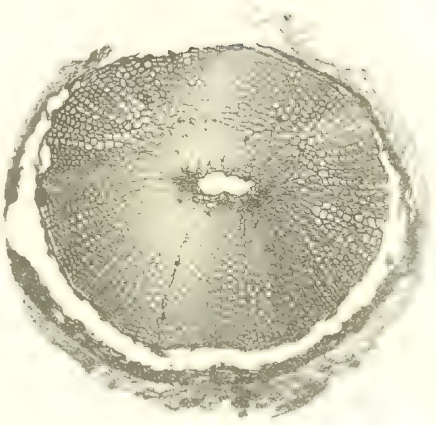


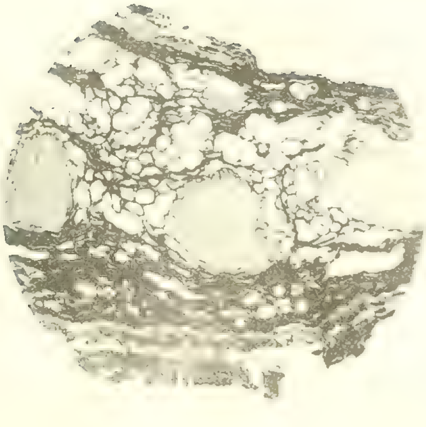












11. FOSSIL FOOTPRINTS OF THE JURA-TRIAS OF NORTH AMERICA.

BY RICHARD SWANN LULL, PH. D.

(Read November 4, 1903.)

> "Sans doute nous devons admirer le fait qu'une créature si insignifiante peut laisser des traces si claires, si nettes et si indélébiles, qui existent depuis des cycles de siècles innombrables, tandis que les efforts les plus grands de l'homme intellectuel lui peuvent survivre à peine et que peu de siècles anéantissent son nom, son langage et ses oeuvres pour toujours." (Winkler, after Deane.)

INTRODUCTION.

THE study of ichnology has practically lain dormant since the death, in 1864, of Edward Hitchcock, the founder of the science and its greatest exponent. Since that time our knowledge of early reptiles, especially the Dinosauria, has arisen and it has seemed wise to undertake anew the study of footprints in the light of modern palaeontology, with the view not only of gaining a greater insight into the nature and structure of the forms which frequented the ancient mud flats and beaches of Triassic days, but also of throwing light upon the correct interpretation of the remains of those evidently allied forms whose bones are known. Thus, on seeing the great collection in the Hitchcock ichnological cabinet of Amherst college, Professor Osborn was at once struck with the possibilities of which it gave promise and suggested to the writer the line of research of which this dissertation is the first fruit.

The writer has had full access, through the courtesy of the authorities of Amherst college and of Dr. Edward Hitchcock, Jr., in particular, to the above named collection and also to that of Mt. Holyoke college. Other lesser collections, namely, those of Rutgers college and of Lafayette college, which contain some of the type specimens, have been placed at the author's disposal, the only regret being that the magnificent gathering of footprints brought together by the late Professor Marsh of Yale university is as yet inaccessible to the student.

Free use has been made of Hitchcock's great works, the Ichnology of New England (**'58**) and the Supplement (**'65**), as well as of the numerous other papers on the subject, due notice of which appears in the proper place. The drawings, with one or two exceptions, have been made by the author directly from nature, their final preparation for publication being the result of Mrs. Lull's skillful and painstaking endeavor. Special acknowledgment is due to Dr. O. P. Hay for his valued counsel in the solution of some vexatious problems of synonymy, but above all for his admirable Bibliography and catalogue of the fossil Vertebrata of North America (:**02**) which proved a great aid in the preparation of the bibliography.

The writer is also under obligations to Prof. A. Smith Woodward, of the British museum, for a superb photograph of Chirotherium tracks, to Prof. C. H. Hitchcock for further notes on some of his species of footprints, to Professor Emerson for notes on the geology of the Connecticut valley, and to many others who, by their suggestions, have aided the work. Finally, to my friend and teacher, Professor Osborn, my gratitude is especially due for his sympathetic advice and criticism and for the great fund of knowledge concerning these early forms, of which he was ever ready to impart.

Historical Sketch.

An excellent résumé of the whole progress of ichnology has been given by C. Winkler in his "Histoire de l'ichnologie" (**'86**), but a sketch of the development of the science, especially in this country, may not be out of place.

Discovery.— Footprints were first discovered in 1812 or 1813 in the Bunter sandstone, at Dumfries, Scotland, but not until 1828 was the first description, that written by Duncan, given to science. The famous Chirotherium footprints from Hildburghausen, in Saxony, were first mentioned in 1834 in a communication by Reinhard Bernhardi to the Neues jahrbuch für mineralogie, and were first described by J. Kaup in the same publication in 1835.

Another very important discovery was that of the Storeton footprint quarry near Liverpool, England, first described by Cunningham, Yates, and Edgerton in the London and Edinburgh philosophical magazine, in 1838. This locality has yielded an interesting Chirotherium of a later stage of evolution than *C. barthi*, and in addition there are numerous tridactyl tracks of which a study is yet to be made.

Before the discovery of the Storeton remains, those of the Connecticut valley had been found, their true nature recognized, and the first notice recorded in the American journal of science and arts, in 1836. Winkler says, in speaking of the former discoveries: "By these impressions of divers feet, the existence of reptiles and of amphibians which have left their traces in the rocks, has been proved; now it is the impressions of the feet of birds which have been found in the new red sandstone of Massachusetts."

While Hitchcock was apparently the first to treat the Connecticut valley impressions from a scientific point of view, yet to Dr. Deane (**'44b**), of Greenfield, Massachusetts, belongs the credit of discovery, though he believed the tracks to be those of a turkey, and did not appreciate the full significance of the remains until Hitchcock had published his views.

Collections.— Extensive collections were made, most of the specimens finding a resting place in the Hitchcock ichnological cabinet which contains most of the type specimens and representatives of almost every known species.

Later collections were formed at Mount Holyoke college and at Yale university. The latter collection, made under the direction of the late Professor Marsh, is said to rival that of Amherst college itself, though the specimens are as yet unavailable for study owing to lack of exhibition space. It is earnestly hoped that provision for the study and display of this collection will soon be made and the results given to science.

Literature.— Three monumental works on the subject of ichnology were published by President Hitchcock during his life and they form the classics of the literature of the science. The first bore the title, "An attempt to discriminate and describe the animals that made the fossil footmarks of the United States, and especially of New England," and was published in the Memoirs of the American academy of arts and sciences, 1848. The second work was the "Ichnology of New England," a large quarto, published in 1858, by the Commonwealth of Massachusetts. This was followed in 1865 by the "Supplement to the Ichnology of New England," also published by the Commonwealth. These are in addition to numerous papers published by Hitchcock in the American journal of science and arts, and elsewhere, in all some eighteen titles.

A posthumous work by Dr. James Deane entitled, "Ichnographs from the sandstone of Connecticut river," published in Boston, in 1861, is a very interesting volume consisting in the main of admirably executed drawings and photographs of the tracks. The memoir itself is incomplete and adds but little to our knowledge of the subject.

Classifications.— An historical review of the various classifications that have been proposed will be of interest in that they show the evolution of the subject from its inception down to the year 1889, when the last important paper was published. The first classification was proposed by E. Hitchcock (**'37b**) and it will be observed that the names were given to the tracks and not to the animals which made them. This classification was as follows: —

ICHNITES.

A. TETRAPODICHNITES.

1. *T. didactylus.*

B. SAUROIDICHNITES.

1. *S. barrattii.*
2. *S. palmatus* (formerly *Ornithichnites palmatus*).
3. *S. minitans.*
4. *S. polemarchius.*
5. *S. tenuissimus.*

C. ORNITHICHNITES.

a. Pachydactyli.

1. *O. giganteus.*
2. *O. tuberosus.*
3. *O. parvulus.*
4. *O. parallelus* (formerly *O. tuberosus*, var. *dubius*).
5. *O. divaricatus.*
6. *O. cuneatus.*

b. Leptodactyli.

1. *O. ingens.*
2. *O. robustus* (*O. ingens minor*).
3. *O. diversus*, var. *clarus.*
   " " " *platydactylus.*
4. *O. deanii.*
5. *O. tenuis.*
6. *O. minimus.*
7. *O. crassus.*
8. *O. minusculus.*
9. *O. tetradactylus.*
10. *O. gracilis.*

Another classification was that published in 1844 (E. Hitchcock, **'44a**) embracing foreign as well as American species.

1. Tetrapodichnites; footprints of quadrupeds, containing among other forms, Chirotherium, *Batrachoidichnites* (*Batrachopus*) *deweyi.*

2. Dipodichnites; footprints of bipeds.

A. In America.
  a. Sauroidichnites; resembling the tracks of saurians. 11 species.
  b. Ornithoidichnites; resembling the tracks of birds.
    1. Pachydactyli, with thick digits. 4 species.
    2. Pachydactylo-pterodactyli, with thick digits having thin edges. 2 species.
    3. Leptodactyli, with long and slender digits. 15 species. In all, 32 species.

B. In Europe.
  1. Tridactyls in Shropshire and Cheshire.
  2. Tridactyls in Saxony.

In 1845, Hitchcock (**'45b**) published a new series of names, those of the animals that made the tracks and not of the tracks themselves. This nomenclature was succeeded later by another, as Hitchcock considered that he had a right to change his published names at will. Following the usage of Hay in his Bibliography and catalogue of the fossil Vertebrata of North America (:**02**), this paper of 1845 is taken as the basis of the true nomenclature of the ichnites, all subsequent names being considered as synonyms and the old track names disregarded. The classification of 1845 is as follows: —

I. STRUTHIONOIDAE.

1.	Eubrontes.	5 species.	(Ornithoidichnites.)

II. PTEROPODIDAE.

2.	Fulicopus.	2 species.	(Ornithoidichnites.)

III. PENTEDACTYLIDAE.

3.	Sauropus.	1 species.	(Sauroidichnites.)

IV. TETRADACTYLIDAE.

4.	Polemarchus.	1 species.	(Sauroidichnites.)
5.	Plectropus.	2 species.	"
6.	Harpedactylus.	1 species.	"
7.	Ancyropus.	2 species.	"
8.	Palamopus.	1 species.	"
9.	Sillimanius.	4 species.	(Ornithoidichnites.)
10.	Triaenopus.	2 species.	(Sauroidichnites.)

V. TRIDACTYLIDAE.

11.	Steropoides.	3 species.	(Ornithoidichnites.)
12.	Argoides.	4 species.	"
13.	Platypterna.	3 species.	"
14.	Calopus.	1 species.	"
15.	Typopus.	1 species.	(Sauroidichnites.)
16.	Batrachopus.	2 species.	(Batrachoidichnites.)

The last classification proposed by Edward Hitchcock is that given in the Ichnology, in 1858, and this remained unchanged until 1889 when his son, Prof. C. H. Hitchcock (**'89b**), brought forth a new one in which dinosaurs were first recognized as the possible makers of many of the tracks. This classification was republished in Professor Emerson's Geology of Old Hampshire county, Massachusetts (**'98**, p. 400–403) and owing to error was the same as that of 1889 though it was supposed to have been revised. In a letter to the present author, dated April 3d, 1903, Professor Hitchcock submits the intended revision of 1898 in which four genera with fifteen species are removed from the Dinosauria and are placed once more with the leptodactylous birds which would seem to be rather a retrogressive step in spite of the fact that the word "birds" is preceded by an interrogation point. C. H. Hitchcock (**'89b**) would call dinosaurs only such as show front feet, heels, or tails. Moreover, he considers birds long legged and dinosaurs short of limb, although short as well as long limbed birds exist, while dinosaurs as a rule were rather long legged and certainly the great majority of cursorial forms among them were capable of long strides when well under way.

E. Hitchcock's classification of 1858 divided the forms into the following groups:—

Group I.— Marsupialoid Animals.

Anomoepus, etc., 3 genera.

Group II.— Pachydactylous or Thick toed Birds.

Brontozoum, Grallator, etc., 3 genera.

Group III.— Leptodactylous or Narrow toed Birds.

1. Tridactylous,—Argozoum, etc. 2. Tetradactylous,— Ornithopus, etc., 4 genera.

Group IV.— Ornithoid Lizards or Batrachians.

Gigantitherium, Plesiornis, etc., 7 genera.

Group V.— Lizards.

Plectropterna, etc., 11 genera.

Group VI.— Batrachians.

Otozoum, etc., 10 genera.

Group VII.— Chelonians.

Chelonoides, etc., 5 genera.

Group VIII.— Fishes.

Ptilichnus, 1 genus.

In all, forty-four genera and ninety-three species. In Charles Hitchcock's classification, while the dinosaurian group was recognized, yet the carnivorous dinosaurs which may be correlated with the *Anchisauridae*, or primitive carnivorous dinosaurs, were still retained under the head of pachydactylous birds, an extremely conservative view; while only such as exhibited either manus or tail were referred to the reptilian group.

The classification proposed in the present memoir, which will be given later, refers by far the greater number of the species to the dinosaurs, though to what order some of the obscure tracks belong is by no means certain; in fact it may never be fully known. Certain of the truly quadrupedal forms may, with fair assurance, be referred to the Proterosauria of Seeley[1] from their very dinosauroid pes, while others, so far as any evidence which the tracks offer is concerned, might as readily be referred to almost any of the reptilian orders. The presence of Stegocephalian Amphibia or Batrachia cannot be definitely proven as yet.

GENERAL DISCUSSION.

Introduction.— In the red and gray sandstones and shales of the Connecticut valley, and in certain parts of New Jersey and elsewhere, have been found numerous indications of the ancient beings which peopled those localities in bygone ages. These indications take the form of impressions of some part of the body of these early forms, either of dermal appendages such as scutes and callosities, or of dragging portions of the body, such as the traces made by the tail; but by far the most numerous of all are the prints of the feet which render to the student a fairly complete knowledge of the size, proportions, and habits of their maker and, coupled with the knowledge gained through other sources, give us a considerable insight into the morphology of the feet and the affinities of the forms themselves.

That both vertebrate and invertebrate creatures were here represented is certain; but, with the exception of the class Reptilia among the former, which group contains by far the greater number of the tracks, it is rather difficult to assign the forms to their proper classes.

It was formerly supposed that certain parallel traces were made by the fins of fishes whose remains are found somewhat abundantly in certain localities. This interpretation has since been doubted and the traces relegated to the group of doubtful genera. Amphibians may have been present, but there are no tracks which can with absolute certainty be referred to them and the same may be said of the birds though the present author has sought earnestly for avian indications. The class Mammalia seems also to be unrepresented.

---

[1] "A very primitive group related to the Rhynchocephalia from which the dinosaurs may have arisen." (Osborn.)

Among the reptile tracks the majority seem to be dinosaurian in origin and are referable to both the Theropoda, or carnivorous dinosaurs, and the Orthopoda, or herbivorous forms; the great Sauropoda, herbivorous quadrupedal forms of the Jurassic, either not having appeared or having been so truly aquatic and of such vast bulk that they could not wander over the shallow water flats and beaches where the tracks were formed. Certain quadrupedal tracks show strong Theropod affinities and were doubtless formed either by primitive dinosaurs or by the Diaptosaurian progenitors of that group which survived side by side with the more specialized forms. Again, certain of the footmarks show lizard-like characters, though no lizards are known from so remote a time; others are Chelonoid while yet others seem to be related to, or at least to resemble, early crocodiles.

Many of the tracks are beautifully preserved, showing even the most delicate tegumentary impressions and it is upon these that the author has spent the larger part of his time in the endeavor to learn the structure of the foot. Other of the remains are in some instances extremely obscure and give little or no insight into their maker's form, but in the revision of the fauna it became necessary to treat them as fully as conditions would permit, but with very unsatisfactory results.

Geological age and conditions.— The geological age of the beds in which the ichnites are found is generally conceded to be upper Triassic, equivalent to the Keuper and Rhaetic of Europe, a correlation which is based upon the remains of fossil plants and of fishes which they contain. From the evidence of the footprints themselves it is apparent that the dinosaurs had already reached a high degree of adaptive radiation and specialization, which would argue against the reference of the formations to any earlier period.

The remains are found in at least two of the ten Triassic areas as enumerated by Dana ('95, p. 741) and of these the classic locality is the valley of the Connecticut river in a belt ranging from the village of Northfield, Massachusetts, to New Haven bay, a distance of one hundred and ten miles, and with a width of about twenty miles.

The New Jersey localities are in the Palisade belt which extends from the Hudson river, through New Jersey, Maryland, and Pennsylvania, to Virginia.

The Connecticut valley belt is clearly of estuarine formation with the tidal ebb and flow of water. It was also subject, locally at least, to conditions of flood which brought down coarser débris from the surrounding country, as the sudden change in the character of certain strata from shale to coarse sandstone gives evidence. An instance of this occurs in the Otozoum beds of South Hadley, Massachusetts, where the layers upon which the animals walked were so soft and fine in texture as to be incapable of preservation while the overlying hard sandstone several inches in thickness preserves upon its under surface the footprints in high relief. This is paralleled in the Chirotherium localities in Hessburg, Saxony, and at Storeton quarry, in England.

Most of the footprint localities were well out in the ancient bay and were evidently tidal flats which were daily left bare by the ebbing waters as the occasional record of a shower of rain associated with the footprints gives evidence. The presence, at times, of ripple marks and other littoral features lends weight to the tidal theory.

Three factors aided in the preservation of these remarkable remains. First, the fierce heat of a tropical sun, for the plant fossils are sufficient evidence of such climatic conditions. Emerson ('**98**, p. 379) says that all of the famous localities were out in the ancient bay in sandstones that rest directly on the back of the broad trap sheets and not very high above them and that the heat which emanated from the not yet cooled lava together with the iron which was liberated by its decomposition constitute two very efficient agents, the second and the third, for the preservation of the impressions.

Skeletal remains.— With the exception of fishes, the actual vertebrate fossils are extremely rare, but few localities having yielded them. Such as have been found are the remains of dinosaurs and they seem to indicate that the great majority of the carcasses which found their way into the water were swept out to sea by the tide and irrevocably lost, or that the conditions were not right for their preservation. The rarity of the remains would argue in favor of terrestrial as opposed to either wholly or partially aquatic habits on the part of these forms.

Dinosaurian characters in the tracks.— The assumption that the majority of the vertebrate tracks are those of dinosaurs seems readily proven though the proof of the non-existence of birds is rather more difficult than the elimination of other vertebrates. The foot characters wherein the birds and the dinosaurs agree are: first, the digitigrade, functionally tridactyl pes, though in both groups the foot is generally structurally tetradactyl. The phalangeal formula, 1st digit, 2; 2d digit, 3; 3d digit, 4; 4th digit, 5, is identical in each group and the order of reduction of the digits is the same, namely: first, V, the outer digit, then I, the inner digit or hallux, and never first, I, as in mammals. Another common character is the length of limb as compared with the length of the foot, a long legged form being indicated by a long stride and narrow trackway. Finally, the bipedal walk as opposed to the sprawling quadrupedal gait of the majority of modern reptiles is an annectant character.

The features which separate the tracks under consideration from those of birds are several, though all do not occur in each instance. They are: first, the presence of a tail trace which is unquestionably reptilian. This may be a continuous serpentine impression or a series of short straight ones as though the appendage were raised at each step, or it may be a continuous, straight line impressing during the whole of the animal's walk or just before sitting on its heels as in the case of *Anomoepus intermedius*. The occasional impression of a manus is another distinguishing character and the presence of irregular dermal scutes or tubercles upon the skin, though rarely leaving a record, is certainly not avian.

Relation of pads to interphalangeal joints.—The generalized arrangement of the pads, which, with the exception of the distal articulation, are mesarthral, that is, they lie opposite the phalanges as in the human hand and not arthral with the pads opposite the joints, as in all lizards and the majority of carinate birds, characterizes the earlier dinosaurs. That this interpretation of the morphology of the foot is correct seems true for several reasons. The foot bones of *Anchisaurus colurus*, which is clearly to be correlated with the track, *Anchisauripus dananus*, will only lie in the impression in one way and that brings the pads mesarthral in position. Hatteria seems to have mesarthral pads, certainly they are not arthral and Hatteria's foot must approximate that of the dinosaurs more than any known form. Finally in certain of the Limicolae, namely *Phalaropus hyperboreus*[1] in which the foot retains its cursorial character without having become specialized for perching, the pads are arranged as in dinosaurs. The rhea has another form of specialization, for here the pads become confluent and hence fewer than the overlying bones, giving no clue to the phalangeal formula, especially on digit IV. It seems probable that among the later Iguanodont dinosaurs there was a coalescence of pads correlated with increase in weight as in the rhinoceros. The tracks of Iguanodon itself, which are known, conform with this belief.

Hitchcock's view that the distal pad of each digit covers both the penultimate and the proximal end of the ungal phalanges is undoubtedly correct. When viewed from the side the ungal phalanx shows a groove running from the point backward midway between the upper and lower borders until it reaches a point about half the length of the bone in a walking digit and farther backward in a grasping one. Another sinuous depression which takes a forward and downward course across the bone defines the hinder limit of the claw sheath, while into the grooves first mentioned, fit ridges on the inner surface of the claw and serve to hold it firmly in place. The fleshy part of the digit extending somewhat beyond the root of the claw thus covers a greater or less portion of the phalanx itself as well as that just within (fig. 1). In cases where

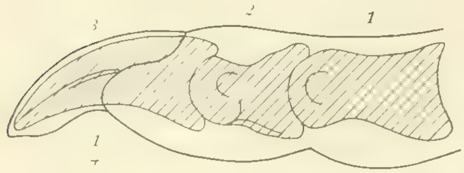


Fig. 1. Digit II of Dimodosaurus viewed in profile with the outline restored to show the relation of the claw and pads to the phalanges. From a cast in the collection of the American museum of natural history. × ¼.

---

[1] Coues, Key to North American birds, 1884, fig. 53 *bis*.

the claw is absent the ungal as well as the penultimate phalanx must lie entirely within the distal pad as in digit I of *Chirotherium barthi* (pl. 72, fig. A).

Prehensile and locomotor terminal claws.—In the less specialized dinosaurs, even among the carnivorous forms, the anterior ungals of the pes do not seem to have borne *prehensile* claws, though such were undoubtedly borne on those of the manus and in all probability upon the hallux as well, as long as the latter remained functional. The increase in curvature of the pedal ungals and the consequent development of the claws seem to be correlated with the reduction of the manus as a prehensile organ, apparently reaching its highest expression in Allosaurus and the later Megalosauria. In Dimodosaurus, a Triassic Megalosaurian dinosaur, the ungal phalanges are less curved than in Allosaurus and the facets indicate that while in the latter the ungal could be flexed through an angle of fully 90°, in the former the possible movement was very slight, as in the later Orthopoda.

Digital reduction in relation to the tracks.—Several stages in the digital reduction in the pes may be observed among dinosaurs, an understanding of which will aid in the interpretation of the tracks.

First, the Anchisaurus (a carnivorous Triassic dinosaur) stage. Here the hallux is complete, insistent, that is, only the tip of the claw touches the ground, rotated backward and probably highly efficient as a grasping claw. Digit V is represented by the proximal half of the metatarsal, and the proximal end of metatarsal II is narrow on its anterior face. This stage is represented by the track genus Anchisauripus.

Second, the Compsognathus (a carnivorous form from the Jurassic of Bavaria) stage. The hallux is complete, slender, insistent, and half rotated, functional though possibly not to so high a degree as in the preceding stage. Digit V is represented by the proximal end of the metatarsal only, and the anterior face of the upper end of metatarsal II is still narrow. This stage is represented among the footprints by Anomoepus, the manus and pes of which are quite like those of Hypsilophodon, though in Anomoepus the pes is much more elongate and slender.

The third stage of digital reduction is that of Allosaurus (a carnivorous Jurassic form) wherein the first metatarsal is not completely ossified in the shaft indicating a partial loss of function on the part of the hallux. This digit is incumbent, that is, its whole length rests on the ground, and it is little more than half rotated. Digit V seems to be obsolete and the proximal anterior face of metatarsal II is the widest. This stage is represented by Gigandipus among the tracks.

Fourth, the Dryosaurus (an herbivorous Jurassic dinosaur) stage in which the hallux is represented by the proximal half of the metatarsal only, the claw being absent. Digit V is also absent. The ichnite Eubrontes may belong to this stage, for the foot seems to be structurally tridactyl, the imprint of the hallux never having been observed.

The fifth stage is that of Ornithomimus, a Cretaceous carnivorous dinosaur, in which both lateral digits are obsolete, and with the loss of metatarsal I, metatarsal IV becomes the widest at the proximal end. Ornithomimus seems to be an aberrant form and strongly suggests the footprint genus Grallator. Most Cretaceous dinosaurs have reached this stage of absolute structural tridactylism.

Digit V is thus the first to suffer reduction being functional in no known dinosaur. Digit I follows, but more slowly, especially in the carnivorous Theropoda where its use as a prehensile claw caused it to be retained longer than in the herbivorous Orthopoda. An interesting compensation is also shown between the widening of the proximal end of metatarsal II as metatarsal V is reduced and in the same manner the widening of metatarsal IV follows the loss of that of the hallux, thus maintaining the width of the ankle joint. Otozoum represents a pro-Anchisaurus stage in its plantigrade foot and well developed, non-rotated hallux. It is more generalized than the foot of any known dinosaur.

Evidences as to gait, speed, and habits.— (*a*) *Non-saltatorial.* The gait of the various creatures which left their impressions on the sandstone is in most instances a true walk or run, generally bipedal, sometimes quadrupedal, and but rarely does one find evidence of a sprawling crawl, such as most modern reptiles exhibit. There is no evidence whatever among the footprints of a leaping dinosaur, that is, one in which both feet leave the ground at the same moment. *Fulicopus lyellianus*, in a fine specimen, no. $\frac{1}{7}$, of the Hitchcock ichnological museum, at Amherst (E. Hitchcock, **'65**, pl. 19), seems to have tried to stop so suddenly as to slide for a considerable distance before overcoming its momentum and this is the nearest approach to evidence in favor of a saltatorial form.

The Anomoepodoid forms, which include Fulicopus with their elongated metatarsi, have a limb whose structure approaches a saltatorial type as much as that of any other dinosaur, with the possible exception of Hallopus a lower Jurassic form, (Marsh, **'96**, p. 153), and the evidence leads one to doubt whether any dinosaurs were truly leaping in gait. Hitchcock (**'58**, p. 57) in speaking of *Fulicopus lyellianus* (*Anomoepus major*) says: "On one specimen in the cabinet we find the impression [of the ischial callosity, *vide infra*] repeated at the distance of ten inches, as if the animal moved by leaps." This serial repetition of the impression may have been made by the animal resting at each step while feeding as the footprints give no evidence of jumping nor is it likely that an animal would take successive leaps of ten inches when its normal stride was two and a half feet!

(*b*) *Semiaquatic habits.* The existence of semiaquatic forms seems to be proven by the presence of a web to the foot in several instances, the most notable being *Otozoum moodii* in which the membrane, if such it were, extended for some distance beyond the tips of the digits, curiously paralleling *Chirotherium barthi* of Saxony (pl. 72, figs. B, G). The fact that both tracks are found in such soft shale that the impression can rarely be preserved lends color to the belief that they were at least semiaquatic in their habits. Another explanation of the web is suggested, namely to give the creature additional support in soft mud which would have its analogy in the snowshoe.

(*c*) *Bipedalism.* Evidence of bipedalism among dinosaurs is shown in many instances. In Anchisauripus the track during swift movement is tridactyl, the hallux impressing only when the creature was stopping or when the mud was especially soft. The tail in this genus never impresses but was evidently used as a counterpoise, or balancing organ.

Anomoepus, though tridactyl and truly bipedal in gait, nevertheless occasionally rested the hands upon the ground and might also drag the tail and impress the hallux for a short distance before stopping.

Otozoum was a huge, bipedal form, plantigrade and tetradactyl in gait, rarely resting the hands and sometimes dragging the tail as did Anomoepus.

Batrachopus was quadrupedal with a tetradactyl, very dinosauroid pes, and a much smaller, functionally tetradactyl manus. The very long, stilted limbs in this genus suggest the Dinosauria as well.

Finally in Chirotherium one finds a truly quadrupedal form, pentadactyl in both the manus and pes though often the former impresses so lightly as to make a tetradactyl track, as the greater part of the creature's weight was borne on the larger hind feet. This illustrates the statement of Osborn (**:00**, p. 796) in which he says that "tridactylism is correlated with rapid bipedal progression, the inner and outer digits suffering reduction." Among modern forms, Chlamydosaurus, an Australian lizard (Kent, **'97**) gives us the best illustration of Osborn's law, though many other lizards, when frightened, run on the hind limbs with the tail held as a counterpoise.

(*d*) *Possible avian footprints.* The difficulty of distinguishing a track thus formed from that of a bird led Baur (**'87**, p. 102) to suppose that Hitchcock was correct in believing that many of the sandstone tracks were made by true birds. It seems to the writer that, with the possible exception of some of the leptodactylous or caved-in tracks whose affinities are very obscure, one can by a method of elimination narrow the possible avian tracks down to the genus Grallator. In this group the relative length of foot to limb seems to be about that of the bustards, but the foot pads are much more specialized in the bird, those of the outer digit having coalesced to form one as in the struthious birds. Otherwise the foot of Grallator and that of Otis are very similar, even to the loss of the hallux. The fact that Grallator is cursorial rather than arboreal does not lessen the possibility of its being a bird, for the use to which the ostrich puts its wings while running suggests the probability of the evolution of wings, in some forms at least, first as an aid to more rapid running, then to support the creature during long soaring leaps, and finally for true flight. It seems necessary to leave the question in this way until further evidence as to the true nature of Grallator is found.

Footprints and taxonomy.— It becomes at once clear to the student of ichnology that while the various footprint species may represent definite stages in the evolution of the foot, the number of definable genera and species must actually be far less than that of the animals which made them. Marsh (**'93**) shows an appreciation of this when he says, in speaking of the genera Anchisaurus and Ammosaurus: "So far as at present known the footprints of the two reptiles would be very similar differing mainly in size." (Compare figs. 4, 7.)

(*a*) *Variations in the impressions left by the same animal.* There are, doubtless, many instances of individual variation among dinosaurs of the same species other than those of age and sex, and in the tracks, additional causes of variation come in, such as the posture or gait of the animal or the character of the surface over which it walked. The first of these factors has a notable illustration in the slab no. $\genfrac{}{}{0pt}{}{1}{1}$, of the Hitchcock museum. On this specimen are impressed among others, two tracks, the one called by Hitchcock the type of *Anomoepus major*, the other that of *Fulicopus lyellianus*, which though referred to different genera, are in all probability the impressions of the same individual! In each case the size, form, and proportions are the same even to peculiar markings, due to injury or some unusual cause, upon the sole of the foot. The difference is mainly in the hinder part of the track due to the fact that in one case the animal was seated upon its heels, raising the posterior part of the foot a little off the ground, while in the other the entire weight of the creature resting on the foot broadened it out especially beneath the metatarsals and brought another pad into the impression (figs. 26, 27).

(*b*) *Influence of the composition and condition of the ground.* The texture of the ground upon which the animal trod, the fineness or coarseness of the sediment and the degree of dryness are important factors. This is beautifully illustrated by the type specimen of *Anomoepus curvatus*, no. $\frac{52}{10}$ of the Hitchcock museum, of which a photograph may be seen in Hitchcock (**'65**, pl. 15, fig. 2). The slab contains five tracks of one animal walking down the beach toward the water, two of the tracks being above the high water mark of the previous tide and three below. That portion of the shore above the mark was drier and the tracks while well formed do not show the pad outlines and other markings as well as do the third and fourth where the surface was smoother and more moist. Finally the fifth track is much deeper and owing to an uneven surface the hinder part of the foot did not impress, altering the entire aspect of the footprint.

The so called "leptodactylous" tracks of Hitchcock were, as a rule, made in such soft mud that the subsequent caving of the sides of the impression has rendered almost unrecognizable certain well known species and as a consequence has given rise to new ones which have added to the difficulty of unraveling the synonymy. Doubtless there were creatures which frequented these soft mud flats whose remains are not found elsewhere, but it is well nigh impossible to fix their true characters. Both "pachydactylous" and "leptodactylous" tracks sometimes occur upon the same slab which may be accounted for by the supposition that time sufficient for the mud to dry out elapsed between the passage of the two animals. The presence of puddles or tide pools would account for a variable degree of dampness within a comparatively small area.

The general rarity of the narrow toed tracks and their abundance in one locality, as at Weathersfield, Connecticut, where the rock is a very fine red shale and must have been exceedingly plastic when the prints were formed, makes it extremely hazardous to erect many genera and species upon such remains.

(*c*) *Variations of age improbable.* It has been argued that one ought to find the tracks of young among the number and that possibly some of the so called species represent the youthful individuals of forms the adults of which made larger impressions. While this may in certain instances be true, it seems hardly probable for several reasons, among which may be mentioned the comparative constancy of size among the many individuals referable to a single group and the rarity of gradational specimens.

In some cases the adult condition of the individual is indicated by the fact that the claw impression is offset some little distance beyond the distal pad, the significance of which can be appreciated by the study of the foot of the cassowary, for example, in which, in the young, the claw and flesh impressions are united, whereas in the adult they are widely separated due to the growth of the claw. It has been suggested that the growth of dinosaurs was like that of trees, continuous throughout life until the senile condition was reached. This is true only of aquatic, poikilothermous forms in which, as some one has said, the energy which, in the bird or land mammal, is used in overcoming gravity and in the production of heat, can be turned into the growth force. The dinosaurs which frequented these shores were either land forms or, in a few cases, as that of Otozoum, possibly semiaquatic and it is further possible that they were warm blooded. Thus it appears highly probable that they were of limited growth.

The Sauropoda which probably had this tree-like growth are entirely absent from the footprint fauna. Hitchcock ('**58**, p. 41) thinks it hardly probable that "very young animals would often frequent such thoroughfares as the localities of footmarks seem to have been . . . . where so many animals resorted, and where in the dearth of food that must sometimes have existed, the young ones must often have been devoured."

It is possible that the tidal flats were seasonally resorted to as breeding places and that the young were brought forth in remote spots where their footprints would not be preserved, possibly some dry, sandy place at a distance from the water. As a reason for the selection of such rookeries Hitchcock (**'58**, p. 19) suggests "that the eruption of the trap produced an island ridge in the waters, and the heat of the cooling rock made it a favorite resort for animals, and rapidly dried and therefore preserved their tracks in such perfection."

TAXONOMIC CHARACTERS.

The following are the characters which are used in the distinction of genera and species in ichnology.

1. Whether bipedal or quadrupedal in gait. Here one finds a gradational series, for the creatures may be absolutely bipedal, never resting the manus upon the ground, or they may be bipedal in gait and rest upon all fours. They may be quadrupedal but with the bulk of the weight borne upon the hind limbs; or they may be truly quadrupedal with a more equable division of the weight over both manus and pes.

2. The presence or absence and the character of a caudal trace. While the absence of this impression is constant in certain genera, as Anchisauripus and Grallator, its presence is a variable character and does not always appear on every specimen. In Selenichnus and one or two other genera it seems always to be present, but it will readily be seen that it depends largely upon the animal's gait, as in running the tail was well raised.

3. The relative size and contrasted characters of the manus and pes are very important points in the correlation of the footprint classification with that of the animals as known from other sources. Fore and hind feet are generally clearly recognizable as such, yet Hitchcock (**'58**, p. 102) in the genus Plesiornis seems to have taken the accompanying tracks of a somewhat smaller bipedal animal for those of the fore feet of a quadrupedal form. The pes seems to be generally in a more advanced stage of evolution than the manus and in the dinosaurs to be larger and much more ornithoid.

4. The distinction of the right and left foot. Where the phalangeal formula is betrayed by the pads, the number of phalanges is always as in birds, one greater than the number of the digit, thus: $\frac{\text{I}}{2}, \frac{\text{II}}{3}, \frac{\text{III}}{4}, \frac{\text{IV}}{5}$. In four toed forms where there is one backwardly pointing toe it is invariably the hallux and hence on the inside of the foot (fig. 7). In the five toed Chirotherium on the contrary the backwardly curved toe, or *pouce* of the French, represents the fifth digit and is upon the outside of the foot (pl. 72, figs. B, D). In the tridactyl or tetradactyl dinosaur tracks the claws of digits II and IV point away

from the axis of the foot while the claw of digit III is invariably bent inward toward the middle of the trackway. These criteria refer to isolated tracks; where there are two or more footprints in a row there is generally no difficulty in distinguishing the right from the left foot.

5. The number of digits is a valuable character for use in systematic work, though frequently the entire number does not impress, or the mark of the hallux is such as to be easily overlooked. The handprints of Anomoepus or of Chirotherium are very likely to be defective because each animal pressed so lightly with the manus.

6. The length of the toes, both actual and relative, the amount of protrusion or exsertion of the middle toe beyond the lateral ones and the distance between the tips of the latter are valuable criteria.

7. The angle of divarication of the toes is a somewhat variable character, that between the lateral ones (digits II and IV) being the most constant. This is measured by drawing lines through the axes of the digits and reading the angles of intersection with a protractor. As these points of intersection rarely coincide, the angle between the lateral toes is generally greater than the sum of the individual angles. It has been quite difficult to make the descriptions given in the present work agree absolutely with those of Hitchcock in this regard even where the same specimens have been measured.

8. The character of the claws, or their absence, is a criterion of great importance. In the dinosaurs the feeding habits have been deduced from the claw structure and hence the separation of the genera into their proper orders is largely based thereon. Thus it is impossible to imagine Anomoepus, with the small rounded claws on manus and pes, as having carnivorous habits, while the pointed claws and powerful hallux of Anchisauripus would place it among the Theropoda even if we did not associate the genus with the carnivorous Anchisaurus. In some cases it is quite difficult to judge, especially of the claws of the anterior digits of the pes, which, as mentioned above, only become curved trenchant weapons in proportion as those of the manus are reduced or lose their efficiency as prehensile organs. One should remember that among herbivorous ungulate mammals the Ancylopoda,[1] and Agriochoerus[2] are bluntly clawed forms, while Mesonyx, a creodont, was hoofed.

9. The presence and character of the metatarsal or "heel" impression found in the *Anomoepodidae* is a very distinctive character and the relative lengths of heel and foot give about the only definable specific distinction between *Anomoepus scambus* and *A. intermedius*.

10. Varying degrees of plantigrady and digitigrady may be noted and may thus be

[1] Beddard, Cambridge natural history, 1902, vol. 10, p. 211.

Wortman, Bull. Amer. mus. nat. hist., 1895, vol. 7, p. 145

defined. Plantigrade is that foot posture in which the whole sole and heel are applied to the ground in normal progression as in Otozoum. The term calcigrade is used by Hitchcock to define a track in which the heel impression is deeper than the anterior part of the foot. The present author would confine its use to a posture as of the sitting Anomoepus which in its progression is digitigrade (see figs. 19 and 20). In a digitigrade foot only the digits and the distal ends of the metatarsals are applied to the ground as in Gigandipus. Anchisauripus has the posterior part of the foot skeleton raised so high as almost to warrant the application of the term semidigitigrade being applied to it. Such a foot posture may lead to a complication of the pads seemingly without reference to the overlying bones.

Summary of taxonomic characters.— (*a*) *Ordinal.* Whether habitually bipedal, occasionally quadrupedal, or habitually quadrupedal. Character of claws, especially of manus. General form of manus and pes.

(*b*) *Generic.* Relative length of foot to limb. Width of trackway. Presence or absence of caudal trace. Relative size and contrasted characters of manus and pes. Number of digits of manus and pes. Position of hallux. Presence and character of metatarsal or heel impression. Varying degrees of plantigrady or digitigrady. Complexity of pads.

(*c*) *Specific.* Length of digits, actual and relative. Size of animal. Angle of divarication of digits. Peculiarities of form.

CLASSIFICATION.

The classification of the forms which made the footprints is a matter of extreme difficulty as the true nature of many of the footprint genera cannot be ascertained in the present state of our knowledge. The best that can be done in the matter is to place the more obvious forms in what seems to be their proper relationship, reserving, for the present, an expression of opinion upon the remainder of the genera. Amphibia must have inhabited the Triassic estuaries but with the possible exception of Shepardia, their tracks cannot be identified as of such, all of the better known forms evidently belonging to the Reptilia.

A scheme of classification based upon that proposed by Osborn (:03a) may be given as follows: —

Class REPTILIA.

Subclass DIAPSIDA Osborn.

Superorder **Diaptosauria** Osborn.

Order? *PROTEROSAURIA* Seeley.

- Batrachopus Hitchcock.
  - *deweyanus* Hitchcock.
  - *dispar* Lull.
  - *gracilis* Hitchcock.
- Batrachopus Hitchcock.
  - *gracilior* Hitchcock.
  - *bellus* Hitchcock.
- Cheirotheroides Hitchcock.
  - *pilulatus* Hitchcock.

Superorder **Dinosauria** Owen.

Order *THEROPODA* Marsh. (Carnivorous dinosaurs.)

- Anchisauripus Lull.
  - *dananus* Hitchcock.
  - *hitchcocki* Lull.
  - *tuberosus* Hitchcock.
  - *exsertus* Hitchcock.
  - *minusculus* Hitchcock.
  - *parallelus* Hitchcock.
  - *tuberatus* Hitchcock.
- Gigandipus Hitchcock.
  - *caudatus* Hitchcock.
- Hyphepus Hitchcock.
  - *fieldi* Hitchcock.
- Grallator Hitchcock.
  - *cursorius* Hitchcock.
  - *tenuis* Hitchcock.
  - *cuneatus* Hitchcock.
  - *formosus* Hitchcock.
  - *gracilis* Hitchcock.
- Stenonyx Lull.
  - *lateralis* Hitchcock.
- Selenichnus Hitchcock.
  - *falcatus* Hitchcock.
  - *brevisculus* Hitchcock.

Order *ORTHOPODA* Cope. (Herbivorous dinosaurs.)

- Anomoepus Hitchcock.
  - *scambus* Hitchcock.
  - *intermedius* Hitchcock.
  - *curvatus* Hitchcock.
  - *crassus* C. H. Hitchcock.
  - *minimus* Hitchcock.
  - *gracillimus* Hitchcock.
- Anomoepus Hitchcock.
  - *cuneatus* C. H. Hitchcock.
  - *isodactylus* C. H. Hitchcock.
- Fulicopus Hitchcock.
  - *lyellianus* Hitchcock.
- Apatichnus Hitchcock.
  - *circumagens* Hitchcock.

- Apatichnus Hitchcock.
    - *minus* Hitchcock.
- Corvipes Hitchcock.
    - *lacertoideus* Hitchcock.
- Eubrontes Hitchcock.
    - *giganteus* Hitchcock.
    - *approximatus* C. H. Hitchcock.
- Eubrontes Hitchcock.
    - *divaricatus* Hitchcock.
    - *platypus* Lull.
- Otozoum Hitchcock.
    - *moodii* Hitchcock.
    - ? *parvum* C. H. Hitchcock.

Order *INCERTAE SEDIS.*

a. Forms habitually bipedal.

- Argoides Hitchcock.
    - *isodactyletus* Hitchcock.
    - *macrodactylotus* Hitchcock.
    - *redfieldianus* Hitchcock.
    - *robustus* Hitchcock.
- Platypterna Hitchcock.
    - *deaniana* Hitchcock.
    - *concamerata* Hitchcock.
    - *digitigrada* Hitchcock.
    - *tenuis* Hitchcock.
    - *delicatula* Hitchcock.
    - *recta* Hitchcock.
- Tarsoplectrus Lull.
    - *angusta* Hitchcock.
    - *elegans* C. H. Hitchcock.
- Plesiornis Hitchcock.
    - *pilulatus* Hitchcock.
    - ? *mirabilis* Hitchcock.
    - ? *giganteus* C. H. Hitchcock.
- Polemarchus Hitchcock.
    - *gigas* Hitchcock.
- Sillimanius Hitchcock.
    - *tetradactylus* Hitchcock.
    - *gracilior* Hitchcock.
- Steropoides Hitchcock.
    - *elegans* Hitchcock.
    - *ingens* Hitchcock.
    - *infelix* Hay.
    - *loripes* Hitchcock.
    - *uncus* Hitchcock.
- Lagunculapes Hitchcock.
    - *latus* Hitchcock.

b. Forms occasionally quadrupedal.

- Xiphopeza Hitchcock.
    - *triplex* Hitchcock.
- Tarsodactylus Hitchcock.
    - *caudatus* Hitchcock.
    - *expansus* C. H. Hitchcock.

Subclass SYNAPSIDA Osborn.

Order *TESTUDINATA*.

(The reference of the following to this order is somewhat doubtful.)

- Chelonoides Hitchcock.
  - *incedens* Hitchcock.
- Amblypus Hitchcock.
  - *dextratus* Hitchcock.
- Helcura Hitchcock.
  - *anguinea* Hitchcock.
  - *littoralis* Hitchcock.
  - *surgens* Hitchcock.
- Ancyropus Hitchcock.
  - *heteroclitus* Hitchcock.

INCERTAE SEDIS.

a. Forms habitually quadrupedal.

- Eupalamopus Hay.
  - *dananus* Hitchcock.
- Palamopus Hitchcock.
  - *anomalis* Hitchcock.
  - *divaricans* Hitchcock.
  - *rogersianus* Hitchcock.
- Exocampe Hitchcock.
  - *arcta* Hitchcock.
  - *minima* Hitchcock.
- Orthodactylus Hitchcock.
  - *floriferus* Hitchcock.
  - *introvergens* Hitchcock.
  - *linearis* Hitchcock.
- Sustenodactylus Lull.
  - *curvatus* Hitchcock
- Antipus Hitchcock.
  - *flexiloquus* Hitchcock.
  - *bifidus* Hitchcock.
- Isocampe Hitchcock.
  - *strata* Hitchcock.
- Shepardia Hitchcock.
  - *palmipes* Hitchcock.
- Comptichnus Hitchcock.
  - *obesus* Hitchcock.
- Arachnichnus Hitchcock.
  - *dehiscens* Hitchcock.
- Triaenopus Hitchcock.
  - *baileyanus* Hitchcock.
- Cunichnoides Hitchcock.
  - *marsupialoides* Hitchcock.

SYSTEMATIC DESCRIPTIONS.

Class REPTILIA.

Subclass DIAPSIDA Osborn.[1]

Superorder **Diaptosauria** Osborn.[1]

Order? *PROTEROSAURIA* Seeley.

Ordinal characters.[2] Quadrupedal in gait; manus generally much smaller than the pes and five fingered though all may not always impress. Pes with four digits, generally dinosauroid in form, though plantigrade. Limbs generally long.

These forms seem to represent survivors of the ancient stem from which the dinosaurs arose; they may, however, represent primitive quadrupedal dinosaurs which had not yet acquired the erect gait.

Family **BATRACHOPODIDAE**.

Family characters. The same as those given for the order. Digits of the pes with acuminate claws.

Genus **Batrachopus** E. Hitchcock. (Frog foot.)

Batrachopus E. Hitchcock, **'45b**, p. 25.

Anisopus E. Hitchcock, **'48**, p. 226.

Anisichnus C. H. Hitchcock, **'71**, p. xxi, (to replace *Anisopus* preoccupied).

Generic characters. Manus probably with five, always with four broad clawless digits, generally directed forward.

Pes four toed; the hallux non-rotated; all of the digits bearing slender acuminate claws; that of the fourth toe may be absent in the impression, possibly also in the foot; third toe the longest. Manus and pes tracks close together and nearly in a right line. Ratio of track to step, one to seven nearly.

This genus was included by Hitchcock under the Loricoid marsupialoids from its supposed likeness to an armored marsupial. Type species, *B. deweyanus*, E. Hitchcock.

---

[1] Osborn, **:03a**.

[2] The characters here given are based entirely upon the tracks; for further definition of the orders, etc., the student is directed to Zittel's Palaeontologie.

Batrachopus deweyanus E. Hitchcock.

Batrachopus deweyanus E. Hitchcock, **'45b**, p. 25.

Anisopus deweyanus E. Hitchcock, **'48**, p. 226 ; **'58**, p. 60, pl. 9, fig. 3 ; pl. 11, fig. 2 ; pl. 43, fig. 1–2 ; pl. 53, fig. 8 ; pl. 58, fig. 11.

Specific characters. Pes: divarication of digits I and II, 12° ; of II and III, 23° ; of III and IV, 6° ; of I and IV, 40°. Length of digit I, .025 m. ; of II, .038 m. ; of III, .043 m. ; of IV, .038 m. ; of the foot, .043 m. Distance between the tips of the lateral toes, .028 m.

Manus: divarication of digits I and II, 53° ; of II and III, 13° ; of III and IV, 18° ; of IV and V, 24° ; of I and V, 107°. Length of digit I, .008 m. ; of II, .020 m. ; of III, .025 m.; of IV, .025 m. ; of V, .015 m. Distance between lateral tips, .019 m. Length of step, .100 to .113 m. Width of trackway, .050 to .075 m.

This is a somewhat variable species, but in at least one specimen, no. $\frac{21}{1}$, of the Hitchcock cabinet, the variation is so great that it has been deemed wise to erect a new species for its reception.

Type specimens: nos. $\frac{26}{5}$ and $_{6}$, of the Hitchcock cabinet on hard gray shale. Type locality not recorded, but the species is reported from Middletown, Connecticut.

Batrachopus dispar sp. nov.

Specific characters. Pes: divarication of digits I and II, 18° ; of II and III, 20° ; of III and IV, 22° ; of I and IV, 60°. Length of digit I, from the middle point of the heel, .046 m. ; of II, .067 m. ; of III, .072 m. ; of IV, .062 m. Distance between lateral tips, .053 m. Length of foot, .073 m. The digits all bear slender claws except the fourth which is clawless. The toes are broad and the heel is of considerable width as the bulk of the weight was borne upon it. Length of step, .230 m.

Manus: but four digits impressing. Divarication of digits I and II, 26° ; of II and III, 68° ; of III and IV, 20° ; of I and IV, 122°. Length of foot, .030 m. Distance between tips of the lateral toes, .028 m. The manus of this form is about equal in size to that of *B. deweyanus*, while the pes is twice as large. The name *dispar* is given on account of the great disparity in size of the fore and hind feet (fig. 2).

The type is no. $\frac{21}{1}$, of the Hitchcock cabinet, on red shale from the Lily pond at Turner's Falls, Massachusetts.

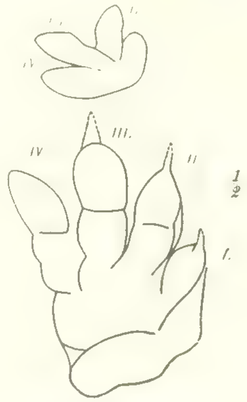
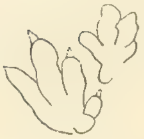


Fig. 2. *Batrachopus dispar* Lull. Impressions of the left manus and pes × ½. Drawn from the type specimen, no. $\frac{21}{1}$, in the Hitchcock cabinet.

Batrachopus gracilis (E. Hitchcock).

Anisopus gracilis E. Hitchcock, **'48**, p. 228, pl. 16, fig. 3–4; **'58**, p. 61, pl. 9, fig. 4; pl. 35, fig. 5; pl. 36, fig. 1–5; pl. 58, fig. 9.

Anisichnus gracilis C. H. Hitchcock, **'89b**, p. 119.



Specific characters. Pes: divarication of digits I and II, 23°; of II and III, 20°; of III and IV, 30°; of I and IV, 73°. Length of digit I, .011 m.; of II, .021 m.; of III, .023 m.; of IV, .031 m. Length of foot, .036 m. Distance between lateral tips, .028 m. All of the digits are clawed. The variation of the figured specimen, no. $\frac{55}{107}$, from Hitchcock's described type is mainly in the divarication, never a constant factor.

Manus: divarication of digits I and II, 23°; of II and III, 25°; of III and IV, 44°; of IV and V, 62°. Length of digit II, .012 m.; of III, .013 m.; of IV, .011 m.; of V, .004 m. The pollex rarely impresses and often the fifth digit is obscure giving practically a functionally tridactyl track. There seems to be a wide range of variation in divarication in the manus as well. Length of step, .209 m. Manus placed just in advance of the pes.

This form is smaller than either of the preceding species (fig. 3).

The type specimen is no. $\frac{42}{3}$, of the Hitchcock cabinet, on a slab of dark shale whose locality is unrecorded. The species is reported from Massachusetts, Connecticut, New Jersey, and Pennsylvania.

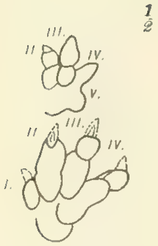


Fig. 3. *Batrachopus gracilis* E. Hitchcock. Successive tracks of right and left manus and pes, showing the relative length of step to foot impression. × ½. From the type specimen, no. $\frac{42}{3}$, of the Hitchcock cabinet.

Batrachopus gracilior (E. Hitchcock).

Anisopus gracilior E. Hitchcock, **'63a**, p. 54; **'65**, p. 6, pl. 1, fig. 3.

Anisichnus gracilior C. H. Hitchcock, **'89b**, p. 119.

Specific characters. Pes: divarication of digits I and II, 14°; of II and III, 11°; of III and IV, 15.5°. Length of digit I, to center of heel, .009 m.; of II, .0125 m.; of III, .014 m.; of IV, .015 m. Length of foot, .015 m. Distance between lateral tips, .012 m.

Manus: divarication of digits I and II, 35°; of II and III, 37°; of III and IV, 11°; of IV and V, 77°. Length of digit I, from center of the rear of the track, .005 m.; of II, .008 m.; of III, .008 m.; of IV, .007 m.; of V, .005 m. Length of foot, .008 m. Length of step, .046 m. Width of trackway, .05 m. Ratio of foot to stride, as one to three.

This form is distinguished from *B. gracilis* by its smaller size and much shorter limbs and wider body, in fact it seems somewhat doubtful whether the species should properly be referred to this genus; it surely is not a typical Batrachopus.

Type specimen, no. $\frac{46}{3}$, of the Hitchcock cabinet, on reddish shale; locality unrecorded.

Batrachopus bellus (E. Hitchcock).

Apatichnus bellus E. Hitchcock, **'58**, p. 101, pl. 17, fig. 6; pl. 35, fig. 8; pl. 45, fig. 6.

Specific characters. Pes: divarication of digits II and III, 30 ; of III and IV, 30 . Length of digit I, .005 m.; of II, .010 to .018 m.; of III, .020 to .025 m.; of IV, .015 to .020 m. Length of foot, .026 m.

Manus: divarication of outer toes, 40°. Length of foot, .013 m. Length of step, .100 to .170 m. Width of trackway, .063 m. Ratio of foot to step, about one to six on the average.

This form is long of limb and strictly quadrupedal in gait though the light impression of the manus is not always discernible. The latter character removes it from Apatichnus and both characters would tend to ally it with Batrachopus. In size it lies between *B. gracilis* and *B. gracilior* but the length of limb would place it nearer the former.

The type is no. $\frac{26}{21}$, of the Hitchcock cabinet, on red shale, from Turner's Falls, Massachusetts.

Genus **Cheirotheroides** E. Hitchcock. (Chirotherium-like.)

Cheirotheroides E. Hitchcock, **'58**, p. 130, pl. 23, fig. 4; pl. 36, fig. 6; pl. 54, fig. 3.

Generic characters. Quadrupedal in gait; feet unequal in size, pes functionally tetradactyl, manus pentadactyl. The three inner digits of the pes generally terminate in pellets, the fourth digit does not. The presence of a fifth digit to the pes is apparently indicated in some specimens, but rarely impresses itself. The limbs are rather short, the ratio of foot to step being as three to four, though the length of step varies.

Cheirotheroides pilulatus E. Hitchcock.

Cheirotheroides pilulatus E. Hitchcock, **'58**, p. 130, pl. 23, fig. 4; pl. 36, fig. 6; pl. 54, fig. 3.

Specific characters. Pes: divarication of digits I and II, 10°; of II and III, 15°; of III and IV, 15°. Length of digit I, .010 m.; of II, .014 m.; of III, .018 m.; of IV, .018 m. Length of foot, .225 m. Distance between lateral tips, .014 m.

Manus: divarication of digits I and II, 57°; of II and III, 60°; of III and IV, 28°; of IV and V, 20°. Length of digit I, .004 m.; of II, .008 m.; of III, .009 m.; of IV, .006 m.; of V, .004 m. Length of step, .320 m. Width of trackway, .570 m.

This species resembles *Batrachopus gracilior* most closely, especially in the short limbs and broad body, but differs therefrom in the pellet-like character of the claws. It may be that the last character is of specific value only and that the two forms mentioned should be brought together under one genus. The present species is extremely rare and is in need of further study before its true character can be learned. It seems best to place it under the Proterosauria because of its pentadactyl manus which Gadow claims is never found among the Amphibia. However, it seems quite far removed from the typical Batrachopus.

Type specimen, no. $\frac{34}{44}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts. This is specimen no. $\frac{34}{31}$ of the Ichnology.

Superorder **Dinosauria** Owen.

Ordinal characters.[1] Bipedal in gait. Pes ornithoid, structurally tri- or tetradactyl, though generally functionally tridactyl. Manus never impressing (Megalosauria), or occasionally resting upon the ground (Orthopoda), but never used for locomotion. Manus pentadactyl. Caudal trace sometimes present.

Order *THEROPODA* Marsh.

Strictly bipedal, digitigrade forms, with a tetradactyl mesaxonic foot, functional, subfunctional, or vestigial hallux. Claws acuminate but not strongly recurved in Triassic forms. Limbs moderately long and trackway narrow. Occasional tail trace.

Family **ANCHISAURIPODIDAE.**

Footprints of dinosaurs of the family Anchisauridae.

Family characters. Bipedal, tetradactylous; hallux, when impressing, rotated to rear, insistent. Well marked phalangeal pads; anterior claws acuminate, but not strongly raptorial. No manus nor caudal impressions. But one genus: Anchisauripus.

Genus **Anchisauripus** gen. nov. (Foot of Anchisaurus.)

Eubrontes E. Hitchcock, **'45b**, p. 23 (in part).

Brontozoum E. Hitchcock, **'47**, p. 50 (in part).

---

[1] Definition applying to Connecticut valley dinosaurs.

Generic characters. Bipedal, tetradactylous; hallux rotated to the rear so as to lie in line with the claw of the second digit, insistent, that is, inserted high on the leg so that only the tip of the claw impresses and that only when the weight is borne on the hinder part of the foot. The hallux evidently bore a well developed, subfunctional, grasping claw. Foot of moderate size with well marked phalangeal pads. Limbs of medium length. Manus and tail never impressing.

This genus is clearly correlated with the Anchisaurus and Ammosaurus of Marsh and is here separated from Hitchcock's genus Eubrontes (Brontozoum) the latter being retained for the larger herbivorous forms which were grouped with the carnivorous species

The type species is *Anchisauripus dananus* (*Brontozoum sillimanium*, in part, of the Ichnology) the track of *Anchisaurus colurus* Marsh.

Anchisauripus dananus (E. Hitchcock).

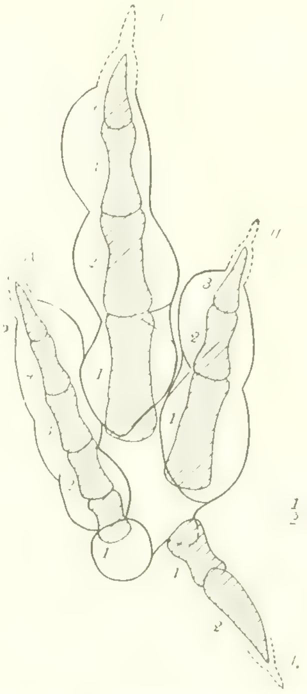


Fig. 4. *Anchisauripus dananus* E. Hitchcock. Impress of the left pes × ½. From the type, no. $\frac{9}{14}$, of the Hitchcock cabinet. The skeleton is based upon that of *Anchisaurus colurus* Marsh.

Eubrontes dananus E. Hitchcock, **'45b**, p. 23 (in part).

Brontozoum sillimanium E. Hitchcock, **'47**, p. 49; **'58**, p. 68, pl. 12, fig. 3; pl. 33, fig. 4–5; pl. 43, fig. 6, (in part).

Specific characters. Divarication of digits I and II, 139°; of II and III, 11°; of III and IV, 18°. Length of digit I, .050 m.; of II, .077 m.; of III, .115 m.; of IV, .088 m. Length of foot, not including the hallux, .153 m.; with the hallux, .187 m. Distance between lateral tips, .067 m. Length of step, from .300 to .560 m. Width of trackway, .115 m.

The type specimen is no. $\frac{9}{14}$, of the Hitchcock cabinet; reddish flagging stone from Middletown, Connecticut. Figured in F. A. Lucas, **:01**, figure 7.

This is undoubtedly the track of *Anchisaurus colurus* Marsh (**'96**, p. 148, pl. 2, fig. 1–3; pl. 3, fig. 1–2) from the exact way in which the bones fit the track (fig. 4).

This is an extremely common and variable species, the variations consisting in size, complexity of heel pads, breadth and divarication of toes, and the shape of the claws. E. Hitchcock (**'58**, p. 69) in speaking of this form says: "I have found it difficult to define the limits of this species and I apprehend that as now given it embraces at least two species. But I have failed to seize upon any distinctive characters between them." It seems to the present author that a division can be made upon the ground of size, though whether this would agree with what Hitchcock had in mind one cannot say. There are, however, certain specimens whose size agrees with what one would expect the pes of *Anchisaurus* (*Megadactylus*) *polyzelus* E. Hitchcock, Jr., to be, judging from the relative sizes of the known part of the skeleton and that of *A. colurus*, and it is proposed to place these specimens under a new species bearing the name of *Anchisauripus hitchcocki* in honor of the great ichnologist.

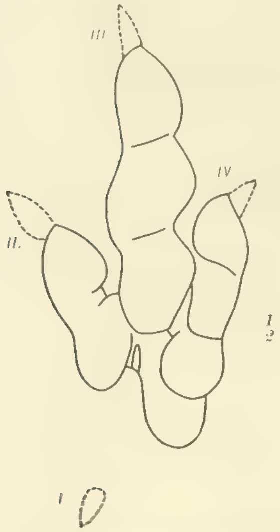


Fig. 5. *Anchisauripus hitchcocki* Lull. Impression of the right pes. × ½. From the type specimen, no. $\frac{56}{1}$, of the Hitchcock cabinet.

Anchisauripus hitchcocki sp. nov.

Synonymy as in *A. dananus*.

Specific characters. Divarication of digits I and II, 138°; of II and III, 19°; of III and IV, 14°; of II and IV, 33°. Length of digit II, .060 m.; of III, .088 m.; of IV, .075 m.; of the foot, exclusive of hallux, .119 m.; including the hallux, .140 m. Distance between lateral tips, .067 m. (see fig. 5).

The type specimen is an individual track, no. $\frac{56}{1}$, of the Hitchcock cabinet, associated with *A. minusculus* and is figured by E. Hitchcock (**'65**, pl. 16, fig. 1). On shale, from the Lily pond, at Turner's Falls, Massachusetts.

This species is correlated with *Anchisaurus* (*Megadactylus*) *polyzelus* E. Hitchcock, Jr., the first dinosaur found in the valley, the type of which is preserved in the Hitchcock ichnological cabinet at Amherst.

Anchisauripus tuberosus (E. Hitchcock).

Eubrontes tuberosus E. Hitchcock, **'45b**, p. 23.

Brontozoum loxonyx E. Hitchcock, **'48**, p. 172, pl. 2, fig. 1–2.

Brontozoum validum E. Hitchcock, **'58**, p. 67, pl. 12, fig. 2; pl. 38–51; pl. 57, fig. 3.

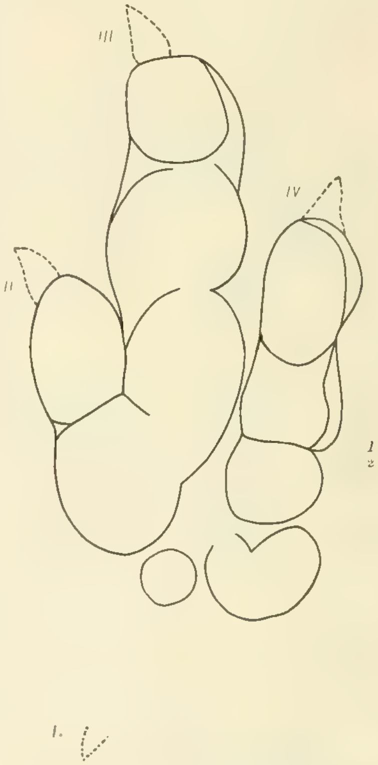


Fig. 6. *Anchisauripus tuberosus* E. Hitchcock. Track of the right pes. × ½. From the type, no. $\frac{41}{73}$, of the Hitchcock cabinet. The hallux impression is restored from another specimen.

Specific characters. Divarication of digits I and II, ? 135°; of II and III, 14°; of III and IV, 13°. Length of digit I, about ? .055 m.; of II, .086 m.; of III, .128 m.; of IV,

.120 m. Length of foot exclusive of hallux, .168 m.; with the hallux, ? .195 m. Length of step, .440 m. Other specimens than the type show measurements somewhat in excess of those given above.

This is a very numerous and variable type, in size between *Anchisauripus dananus* and *A. exsertus*, with no marked peculiarities other than size to distinguish it from either. The type specimen, no. $\frac{31}{73}$, of the Hitchcock cabinet, a superb track, has unfortunately been trimmed in such a way as to destroy the impression of the first claw, but the basal pad of the hallux is clearly impressed. It is figured in the Ichnology on plate 57, figure 3. Specimen no. $\frac{16}{1}$, while somewhat larger, gives all of the characters, including the hallux.

Type, no. $\frac{31}{73}$, of the Hitchcock cabinet, on red shale from Turner's Falls, Massachusetts (fig. 6).

Anchisauripus exsertus (E. Hitchcock).

Brontozoum exsertum E. Hitchcock, **'58**, p. 67, pl. 12, fig. 1; pl. 40, fig. 3.

Specific characters. Based on no. $\frac{54}{1}$. Divarication of digits I and II, 75°; of II and III, 20°; of III and IV, 20°. Length of digit I, .075 m.; of II, .117 m.; of III, .161 m.; of IV, .153 m. Length of foot, exclusive of hallux, .226 m.; including the hallux, .265 m. Length of step in no. $\frac{1}{6}$ (a somewhat larger specimen), .922 m.

The real distinction between this species and *A. tuberosus* seems to be one of size only, for the character which gives the name "*exsertus*," that of the unusual projection of the middle toe beyond the lateral ones, is not always manifest. This species is correlated with *Ammosaurus major* Marsh (**'96**, p. 147, pl. 3, fig. 3–6).

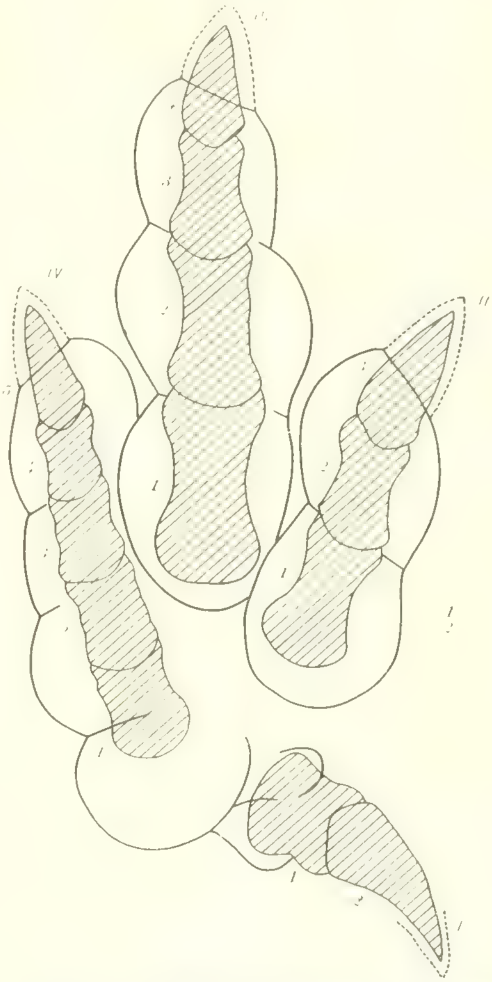


Fig. 7. *Anchisauripus exsertus* E. Hitchcock. Imprint of the left pes × ½. From no. $\frac{54}{1}$, of the Hitchcock cabinet. The bone restoration is after that by Marsh of *Ammosaurus major* Marsh.

Type specimen, no. $\frac{16}{6}$, of the Hitchcock cabinet, on gray micaceous sandstone from Smith's Ferry, Massachusetts (fig. 7, of no. $\frac{54}{1}$).

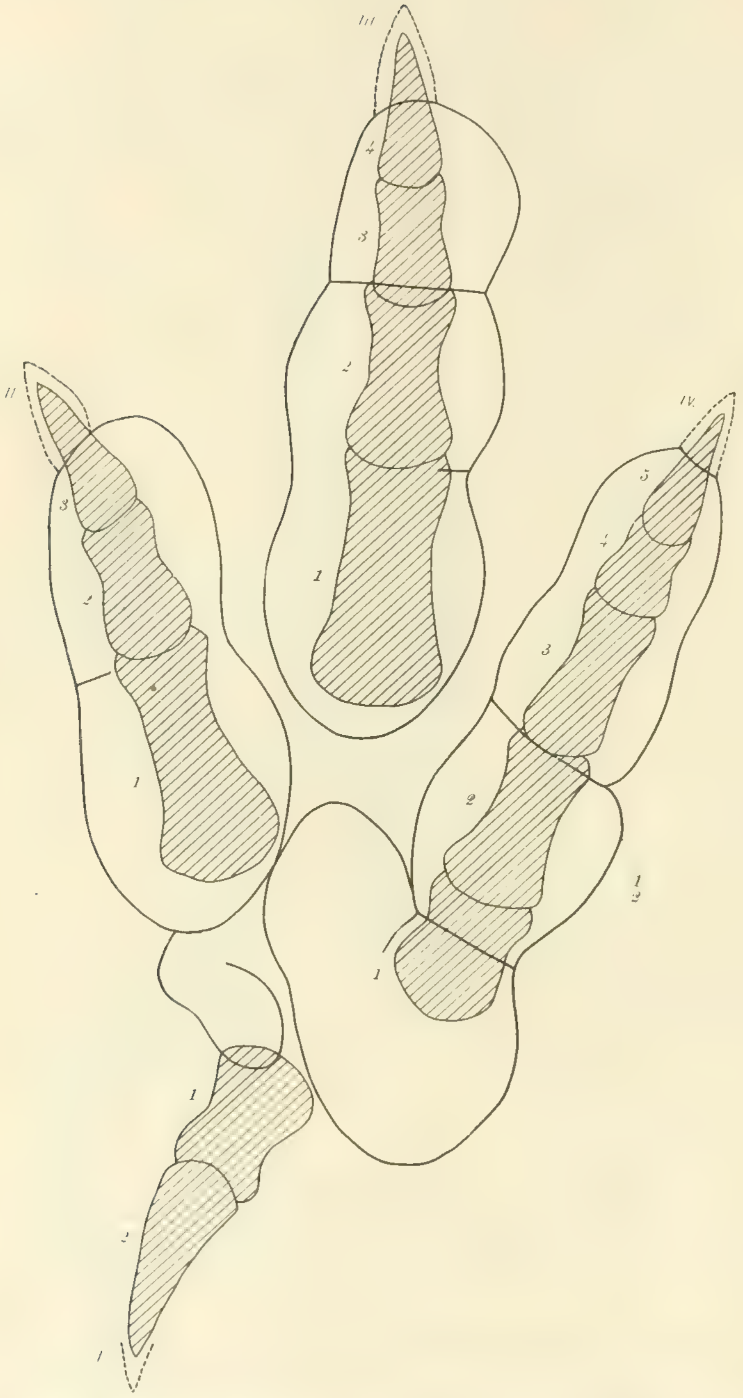


Fig 8. *Anchisauripus minusculus* (E. Hitchcock). Track of the right pes with a restoration of the bones of the foot. × ½. Drawn from the type, no. $\frac{16}{1}$, in the Hitchcock cabinet.

Anchisauripus minusculus
(E. Hitchcock).

Brontozoum minusculum E. Hitchcock, **'58**, p. 65, pl. 11, fig. 1; pl. 40, fig. 2; pl. 41, fig. 1; pl. 42, fig. 3; pl. 57, fig. 2.

Specific characters. Divarication of digits I and II, 140°; of II and III, 24°; of III and IV, 24.5°. Length of digit I, .100 m.; of II, .158 m.; of III, .192 m.; of IV, .223 m. Length of foot, exclusive of the hallux, .307 m.; including the hallux, .374 m. Length of step, 1.000 m.

This magnificent form is the largest of the genus and indicates an animal about twice the size of *Anchisaurus colurus*, which would give it a length of about fourteen feet.

The type specimen, the one here figured (fig. 8), is no. $\frac{16}{1}$, from the Hitchcock cabinet, on fine red shale from the Lily pond at Turner's Falls, Massachusetts.

Anchisauripus parallelus
(E. Hitchcock).

Grallator parallelus E. Hitchcock, **'65**, p. 7, pl. 5, fig. 1.

Specific characters. Divarication of digits I and II, 14°; of II and III, 12°; of III and IV, 6.5°. Length of digit I, .067 m.; of II, .079 m.; of III, .120 m.; of IV, exclusive of "heel" pad, .090 m. Length of foot exclusive of the hallux, .165 m.; including the hallux, .240 m. Length of step, .260 m.

This form is evidently not a Grallator from the shortness of step and the wide trackway. The presence of the hallux removes it from Grallator and associates it with Anchisauripus, though the presence of the three heel pads separates it from *A. dananus*, its nearest ally in point of size. It is also peculiar in the slight divarication of the toes, hence the specific name (fig. 9).

Type, no. $\frac{54}{8}$, of the Hitchcock cabinet, on red sandstone from Gill, Massachusetts; also reported from New Jersey.

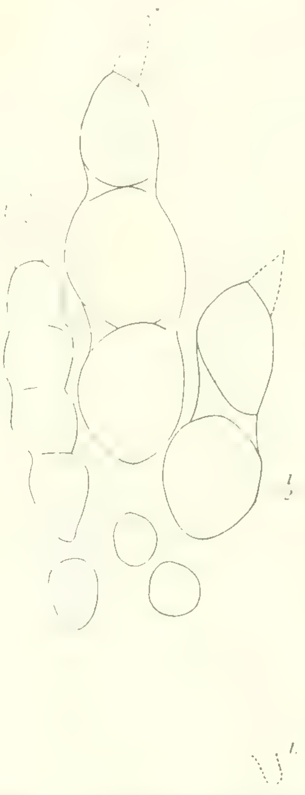


Fig. 9. *Anchisauripus parallelus* (E. Hitchcock). Impression of the left pes × ½. From the type, no. [illegible], of the Hitchcock cabinet.

Anchisauripus tuberatus (E. Hitchcock).

Brontozoum tuberatum E. Hitchcock, '58, p. 66, pl. 11, fig. 2; pl. 52, fig. 7.

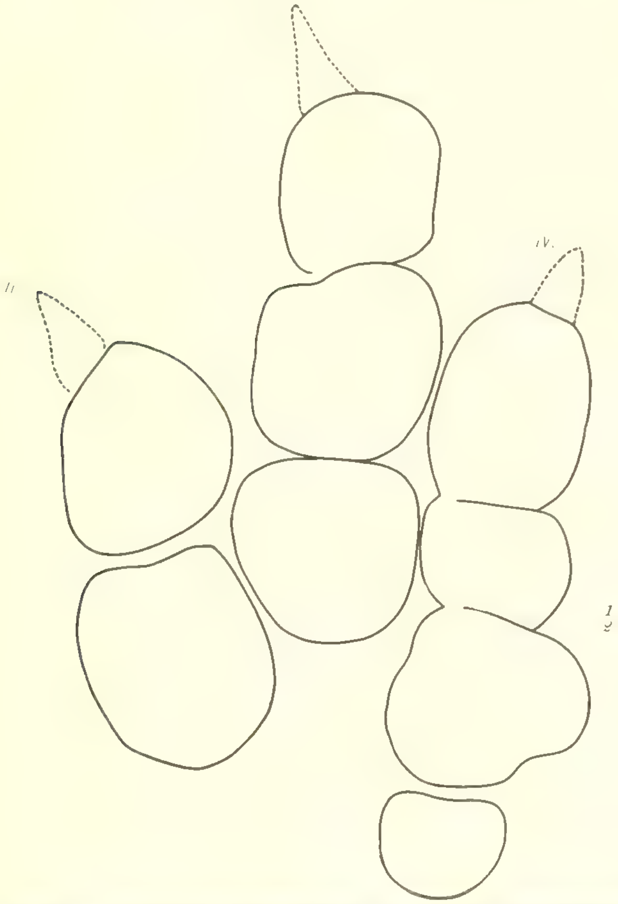


Fig. 10. *Anchisauripus tuberatus* (E. Hitchcock). Impress of the right pes × ½. From the type, no. [illegible], in the Hitchcock cabinet.

Specific characters. Divarication of digits I and II, not known; of II and III, 17°; of III and IV, 8°. Length of digit II, .140 m.; of III, .172 m.; of IV, .107 m. Length of the foot, exclusive of hallux, .249 m. Distance between lateral tips, .152 m.

This species resembles *A. exsertus* in size, being but little larger, but the two forms are readily distinguished by the broad tuberous phalanges of the one in question. In general character, the foot is annectant between Anchisauripus and Eubrontes, the acuminate claws and small size alone among the known characters affiliating it with the former. Unfortunately, the type specimen, no. $\frac{27}{17}$, has been so trimmed as to destroy the hallux impression if it were present so that the presence or absence of this characteristic mark cannot be ascertained (fig. 10).

The type, no. $\frac{27}{17}$, of the Hitchcock cabinet, is on red shale from Turner's Falls, Massachusetts.

Family **GIGANDIPODIDAE**.

Family characters. Large bipedal forms. Tetradactyl, hallux half rotated, incumbent. Foot flatly digitigrade. Claws acuminate. No manus impression. Caudal trace sinuous and continuous. Genera: Gigandipus, possibly also Hyphepus.

Genus **Gigandipus** E. Hitchcock. (Giant foot.)

Gigadipus E. Hitchcock, **55**, p. 417 (no description).
Gigandipus E. Hitchcock, **'56**, p. 97.
Gigantitherium E. Hitchcock, **'58**, p. 93.

Generic characters. Bipedal, tetradactyl, hallux incumbent, that is, inserted low on the leg so that its whole length is on the ground; rotated at right angles to the second toe. Hallux but feebly developed. Foot with distal ends of metatarsals upon the ground in contrast to Anchisauripus in which the foot rests upon the toes only. Claws acuminate; that of digit II especially strongly developed. Tracks nearly in a right line. Caudal trace sinuous and continuous.

The foot of this form agrees very closely in structure with that of Allosaurus (Osborn, **:00**, p. 785, fig. 4) and it was from the limb of that genus (American museum of natural history, fossil reptile collection, no. 290) that the studies for the bone restoration of Gigandipus were made.

Gigandipus caudatus E. Hitchcock.

Gigadipus caudatus E. Hitchcock, **'55**, p. 417 (no description).
Gigandipus caudatus E. Hitchcock, **'56**, p. 97, text figs.
Gigantitherium caudatum E. Hitchcock, **'58**, p. 93, pl. 16, fig. 1–2; pl. 44, fig. 4.

Specific characters. Divarication of digits I and II, 98°; of II and III, 22°; of III and IV, 30°. Length of digit I, .080 m.; of digit II, to metatarsal pad, .215 m.; including the pad, .280 m.; of III, to metatarsal pad, .275 m.; of IV, to the pad, .290 m.;

including the metatarsal pad, .343 m. Length of foot, .445 m. Distance between the tips of the lateral toes, .285 m. Length of step, 1.020 m. Width of trackway, .305 m.

Although this is one of the largest of the Connecticut valley tracks, that of Allosaurus would far exceed it in size for the estimated length of the footprint of the latter would be at least .720 m., as against .445 m. for the Gigandipus.

Type specimens, nos. $\frac{9}{9}$ and $\frac{9}{10}$, of the Hitchcock cabinet, on reddish shale from the Lily pond, Turner's Falls, Massachusetts (fig. 11).

The second species of Gigandipus, the *G. minor* of Hitchcock, has been removed to Apatichnus for which it seems to possess greater affinities.

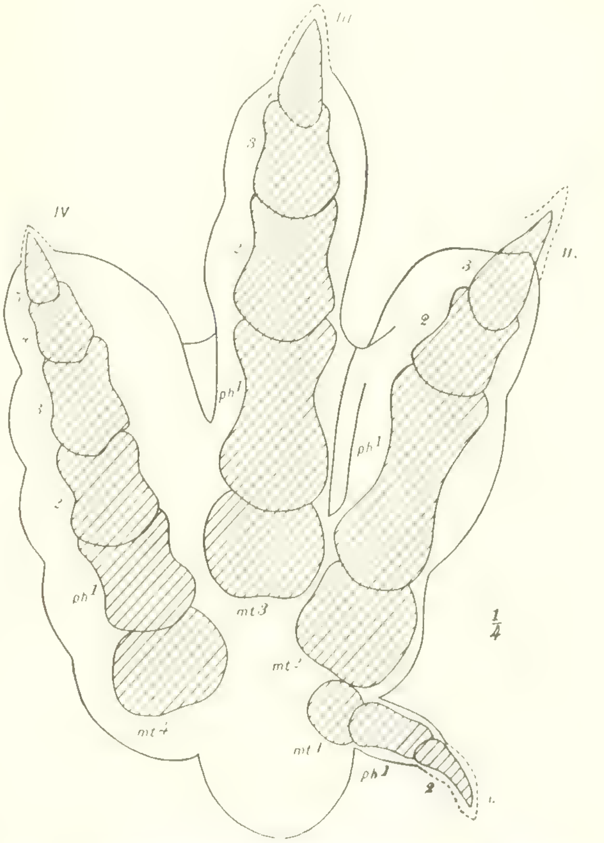


Fig. 11. *Gigandipus caudatus* E. Hitchcock. Imprint of left pes × ¼. From the type specimen, no. $\frac{9}{10}$, in the Hitchcock cabinet. The bone restoration is based upon the foot of Allosaurus, slightly modified from the mounted specimen, no. 290, of the fossil reptile collection of the American museum of natural history.

Genus **Hyphepus** E. Hitchcock. (Web foot.)

Hyphepus E. Hitchcock, **'58**, pp. 97, 189.

Generic characters. Bipedal, tetradactylous track. Hallux incumbent, curving sharply backward. There seems to be a web between the anterior toes and they are apparently clawless, except the third. No phalangeal pads are visible on any of the specimens. Caudal trace present, generally passing through the footprints.

This form occurs at the same horizon with Gigandipus, which it resembles except for its smaller size, the presence of the web and the apparently clawless condition of the lateral digits. It is placed provisionally near Gigandipus though the relationship may not be a very close one.

Hyphepus fieldi E. Hitchcock.

Hyphepus fieldi E. Hitchcock, **'58**, pp. 97, 189, pl. 17, fig. 2; pl. 35, fig. 11; pl. 41, fig. 2; pl. 42, fig. 2.

Specific characters. Divarication of digits I and II, 118°; of II and III, 23°; of III and IV, 28°; of II and IV, 50°. Length of digit I, .026 m.; of II, .077 m.; of III, .078 m.; of IV, .083 m. Length of foot, .128 m. Distance between lateral tips, .071 m. Length of step, .153 m. Width of trackway, .135 m.

Type, no. $\frac{1}{3}$, of the Hitchcock cabinet on micaceous shale from Turner's Falls, Massachusetts.

Family **GRALLATORIDAE**.

Family characters. Small bipedal forms; footprint tridactyl, limbs very long; no manus nor caudal impression. Genus: Grallator; possibly also Stenonyx.

Genus **Grallator** E. Hitchcock. (One who goes on stilts.)

Grallator E. Hitchcock, **'58**, p. 72.

Generic characters. Bipedal, tridactyl tracks; tail trace absent (an apparent exception to this in a specimen referred to *Grallator gracilis*); long limbs and small compact feet. Claws acuminate, moderately developed.

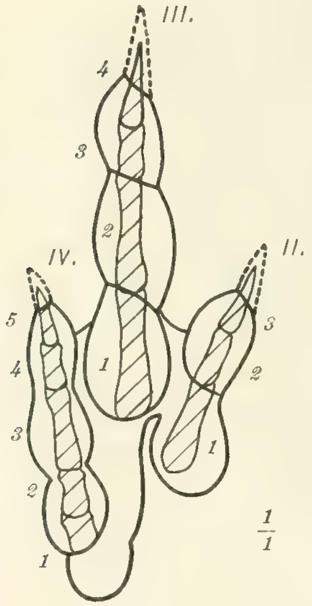


Fig. 12. *Grallator cursorius* E. Hitchcock. Impression of the left pes. × $\frac{1}{1}$. With a restoration of the skeleton. Drawn from no. $\frac{4}{1}$ of the Hitchcock cabinet.

This genus is distinguished from Anchisauripus, which it most closely resembles, by the length of limb, smallness of track and the absence of a hallux. It suggests in proportions the Cretaceous genus, Ornithomimus, and is about the only group of pachydactylous tracks which could possibly be referred to birds, some species suggesting the bustards though in the latter group the pads on digit IV are specialized by coalescence and all seem to be arthral as opposed to the mesarthral pads of Grallator. The association of the long limbed Grallator with the amphibious Otozoum suggests possible wading habits on the part of the former.

Type species, *Grallator cursorius* E. Hitchcock.

Grallator cursorius E. Hitchcock.

Grallator cursorius E. Hitchcock, **'58**, p. 72, pl. 13, fig. 3; pl. 58, fig. 4.

Specific characters. Divarication of digits II and III, 14°; of III and IV, 12°; of II and IV, 26°. Length of digit II, .035

m.; of III, .055 m.; of IV, .045 m. Length of foot, .079 m. Distance between lateral tips, .031 m. Projection of the middle toe beyond the others, .033 m. Length of step, .610 m., giving a ratio of foot to step of about one to eight. Width of trackway, .050 m.

The figured specimen, no. $\frac{4}{1}$, of the Hitchcock cabinet, is the type. The specimen is in high relief upon coarse sandstone from South Hadley, Massachusetts. It occurs in association with *Otozoum moodii* and *Anchisauripus dananus*. It is also reported from New Jersey (figs. 12 and 13).

Grallator tenuis E. Hitchcock.

Grallator tenuis E. Hitchcock, **'58**, p. 73, pl. 13, fig. 4; pl. 53, fig. 5.

Specific characters. Divarication of digits II and III, 15° to 25°; of III and IV, 25° to 28°; of II and IV, 40° to 45°. Length of digit II, .030 m.; of III, .049 m.; of IV, .045 m. Length of foot, .073 m. Distance between lateral tips, .037 m. Length of step, .195 m. Width of trackway, .063 m.

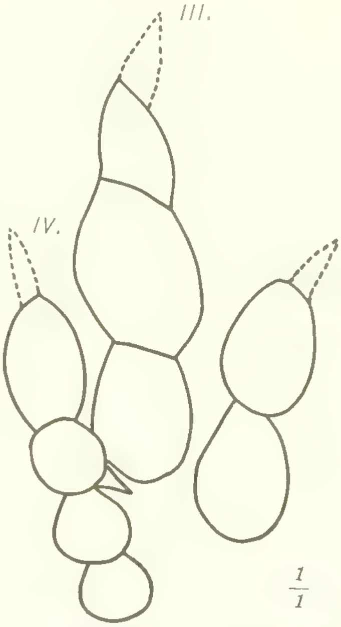


Fig. 13. *Grallator cursorius* E. Hitchcock. Impression of the left pes. × $\frac{1}{1}$. From no. $\frac{4}{1}$, of the Hitchcock cabinet.

The chief distinctions between this form and *G. cursorius* are the shorter stride and greater divarication of the toes of the present species. Both of these are variable quantities and future research may prove the species to be synonymous in which case *G. cursorius* would have priority.

The type specimens are nos. $\frac{12}{3}$ and $\frac{12}{4}$, of the Hitchcock cabinet, counterparts, from Turner's Falls, Massachusetts. The slabs are red shale and were found in close proximity to the trap. The figured specimen is no. $\frac{17}{4}$, of the Hitchcock cabinet (fig. 14). The species is also reported from Connecticut and New Jersey.

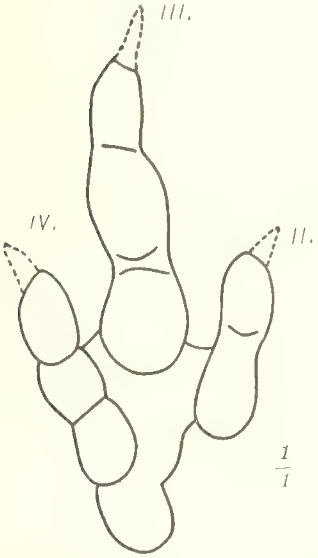


Fig. 14. *Grallator tenuis* E. Hitchcock. Track of the left pes. × $\frac{1}{1}$. From no. $\frac{17}{4}$, of the Hitchcock cabinet.

Grallator cuneatus E. Hitchcock.

Grallator cuneatus E. Hitchcock, **'58**, p. 74, pl. 13, fig. 6; pl. 39, figs. 1, 3; pl. 41, fig. 1–2.

Specific characters. Divarication of digits II and III, 23°; of III and IV, 23°; of II and IV, 46°. Length of digit II, .063 m.; of III, .081 m.; of IV, .074 m. Distance between lateral tips, .080 m. Length of foot, .125 m. Length of step, .460 to .550 m. Width of trackway, .090 m.

This form, while a true Grallator, is quite similar to *Anchisauripus dananus*, but is distinguished from the latter by the greater projection of the middle toe and the generally cuneiform shape of the foot which is heightened by the bending outward of the lateral claws.

The type is no. $\frac{25}{1}$, of the Hitchcock cabinet, on red shale from the Lily pond at Turner's Falls, Massachusetts. Figured specimen, no. $\frac{17}{1}$, of the Hitchcock cabinet, from Turner's Falls (fig. 15).

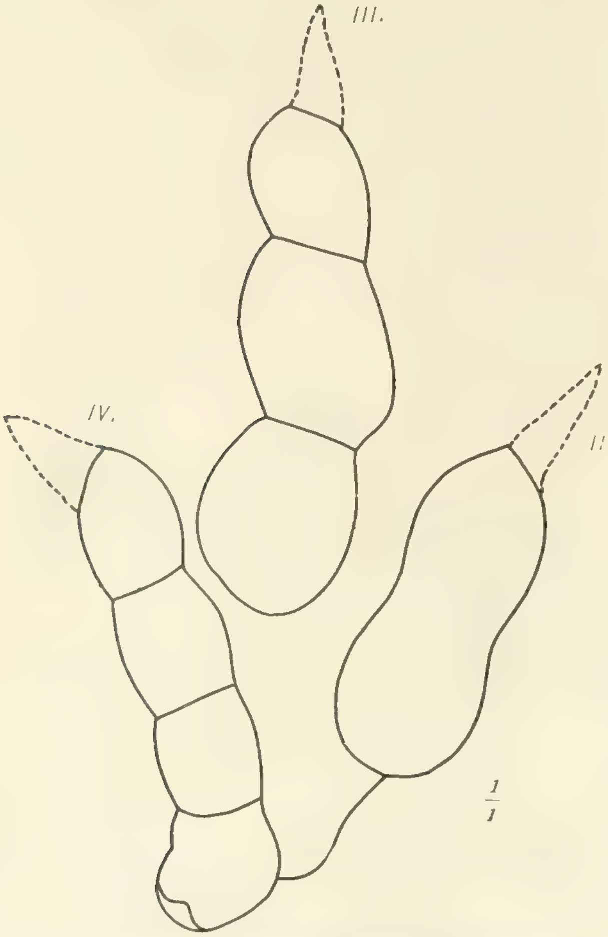


Fig. 15. *Grallator cuneatus* E. Hitchcock. Impression of the left pes. × $\frac{1}{1}$. From no. $\frac{17}{1}$, of the Hitchcock cabinet.

Grallator formosus E. Hitchcock.

Grallator formosus E. Hitchcock, **'58**, p. 75, text fig. 1 on p. 77.

Specific characters. Divarication of digits II and III, 11.5°; of III and IV, 21.5°; of II and IV, 33°. Length of digit II, .075 m.; of III, .118 m.; of IV, .114 m. Distance between lateral tips, .110 m. Projection of middle toe beyond the lateral ones, .070 m. Length of foot, .172 m. Length of step, .655 m.

This is very large for a Grallator, but is long of limb and lacks a hallux on all known specimens. It resembles *G. cuneatus*, differing from the latter chiefly in size. It approaches very near *Anchisauripus dananus* and may prove to be identical at any rate with some of the specimens referred to that species.

Type specimen, no. $\frac{3}{1}$, of the Hitchcock cabinet, shale from South Hadley, Massachusetts (fig. 16), associated with *Otozoum moodii*.

Grallator gracilis C. H. Hitchcock.

Grallator gracilis C. H. Hitchcock, in E. Hitchcock, **'65**, p. 8, pl. 9, fig. 7.

Specific characters. Divarication of digits II and III, 22° to 23°; of III and IV, 14°

to 16°; of II and IV, 35° to 40°. Length of digit II, .026 m.; of III, .035 m.; of IV, .030 m. Distance between lateral tips, .027 m. Length of foot, .045 m. Projection of middle toe beyond the lateral ones, .017 m. Length of step, .315 m.

Charles Hitchcock's character of the non-extension of the inner toe so far as the outer one seems to be inconstant for they are about equal in extent in the present author's figure, from no. $\frac{23}{8}$ (Hitchcock cabinet). This, one of the most diminutive of dinosaur tracks, represents a foot about two thirds the length of that of Compsognathus of the lower Kimeridgian limestone of Bavaria, the smallest known form.

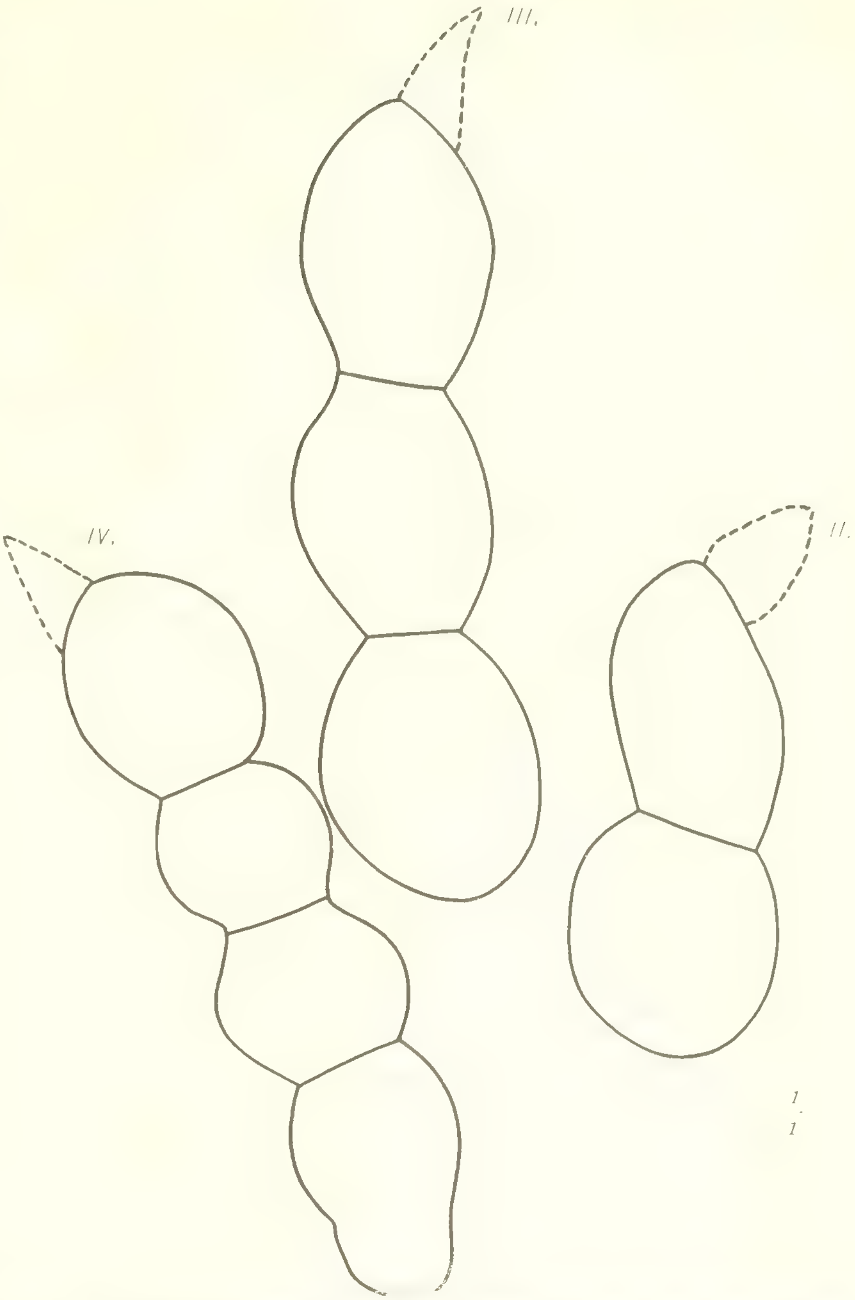


Fig. 16. *Grallator formosus* E. Hitchcock. Imprint of the left pes. From the type specimen, no. $\frac{17}{2}$, of the Hitchcock cabinet.

The type is no. $\frac{17}{2}$, of the Hitchcock cabinet, on red shale from Turner's Falls, Massachusetts, and the figured specimen is no. $\frac{23}{8}$ from the same locality (fig. 17). The species is reported from Massachusetts and New Jersey.

Genus **Stenonyx** nom. nov. (Narrow claw.)

Leptonyx E. Hitchcock, **'65**, p. 8 (name preoccupied).

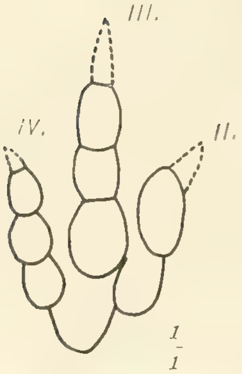


Fig. 17. *Grallator gracilis* E. Hitchcock. Impression of the left pes. × $\frac{1}{1}$. From no. $\frac{2}{8}$, of the Hitchcock cabinet.

Generic characters. Bipedal, tridactyl, digitigrade track, very minute. With thick toes and long slender claws and distinct phalangeal pads. Length of limb unknown as the genus is known only from two isolated tracks. There is no tail trace.

Stenonyx lateralis (E. Hitchcock).

Leptonyx lateralis E. Hitchcock, **'65**, p. 8, pl. 5, fig. 3.

Specific characters. Divarication of digits II and III, 32°; of III and IV, 28°; of II and IV, 60°. Length of digit II, .015 m.; of III, .021 m.; of IV, .021 m. Distance between lateral tips, .021 m. Length of foot, .030 m.

This species seems to approach most nearly to *Grallator gracilis* but is much smaller, and has more slender claws which arise from the median side of digits II and III and from the outside of digit IV; hence the specific name.

Type, no. $\frac{47}{40}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Genus **Selenichnus** E. Hitchcock. (Moon track.)

Selenichnus E. Hitchcock, **'58**, p. 133.

Generic characters. Bipedal, tridactylous. Inner toe rarely distinct. A continuous caudal trace, but slightly sinuous. Tracks nearly in line and without pads or claws.

Selenichnus falcatus E. Hitchcock.

Selenichnus falcatus E. Hitchcock, **'58**, p. 133, pl. 23, fig. 8; pl. 60, fig. 8.

Specific characters. Pes: divarication of digits cannot be measured. Length of digits from extremity of the heel: of II, .036 m.; of III, .072 m.; of IV, .056 m. Length of foot, .072 m. Width of foot, .018 m. Length of step, .090 m. The feet turn outward so that the heels are in line, the tail trace usually passing through them. The toes curve inward.

This is a very striking track and though obscure as to details is readily recognizable. It was apparently formed by a small dinosaur of unknown affinities.

Type specimens are nos. $\frac{42}{6}$ and $\frac{42}{7}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Selenichnus breviusculus E. Hitchcock.

Selenichnus breviusculus E. Hitchcock, **'58**, p. 134, pl. 23, fig. 9; pl. 60, fig. 7.

Specific characters. Pes: length of foot, .046 m.; length of step, .058 m. Width of trackway, .038 m.

This form is found at Turner's Falls, Massachusetts, associated with *S. falcatus* and as Hitchcock says, "may be the young of that species."

Type, no. $\frac{44}{10}$, of the Hitchcock cabinet, a beautiful slab of twenty-three tracks passing in a curved line across the surface.

Order *ORTHOPODA* Cope. (*Predentata* Marsh.)

Ordinal characters. Bipedal dinosaurs, with a mesaxonic, generally digitigrade, tetradactyl or tridactyl foot, armed with more or less blunted claws. The foot ranges from the plantigrade, functionally tetradactyl type of Otozoum, through the digitigrade (occasionally calcigrade while resting) and functionally tridactyl pes of Anomoepus, to the digitigrade, probably structurally tridactyl pes of Eubrontes. The manus is pentadactyl with blunt claws and, while occasionally touching the ground in the resting position, is never used for locomotion; it is considerably smaller than the pes. A caudal trace is occasionally present in some genera.

Family **ANOMOEPODIDAE**.

Family characters. Bipedal in gait, the manus impressing only when resting. Pes tetradactyl, digitigrade with elongate metatarsal segment upon which the animal sits (calcigrade) while at rest. Hallux half rotated, insistent, and subfunctional, but rarely impressing. Pes ornithoid.

Manus pentadactyl, the digits ranging through an angle of 180°. Phalangeal formula: 2. 3. 4. 3. 2. Claws bluntly rounded.

The proportions, except for the elongated metatarsals, and the conformation of the feet and claws, seem to correlate this group with the Wealden predentate dinosaur, Hypsilophodon, which, because of its toothed premaxillary, the generalized character of the teeth and other reasons, Osborn[1] believes to represent the Triassic Orthopoda more nearly than any other known form. There are at least two genera which exhibit all of the family characters and others which are evidently nearly related. Genera: Anomoepus, Fulicopus, Apatichnus; possibly Corvipes, and others.

[1] Osborn, Columbia university lectures, 1903

Genus **Anomoepus** E. Hitchcock. (Unlike foot.)

Anomoepus E. Hitchcock, **'48**, p. 220.

Generic characters. In addition to the family characters above mentioned, this genus may be readily recognized by its very characteristic foot in which the toes are quite widely divergent, especially digit IV. There is also a doubling of many of the lines over the articulations of the phalanges similar in appearance to those of the human hand. Limbs only moderately long; when resting, considerable weight is borne on the hand, a point of difference with the succeeding genus. There is an occasional tail trace and ischial callosity impression. There is also a pad on the sole of the foot in line with and in addition to the four which are usually found on digit IV. The type species is *A. scambus* E. Hitchcock.

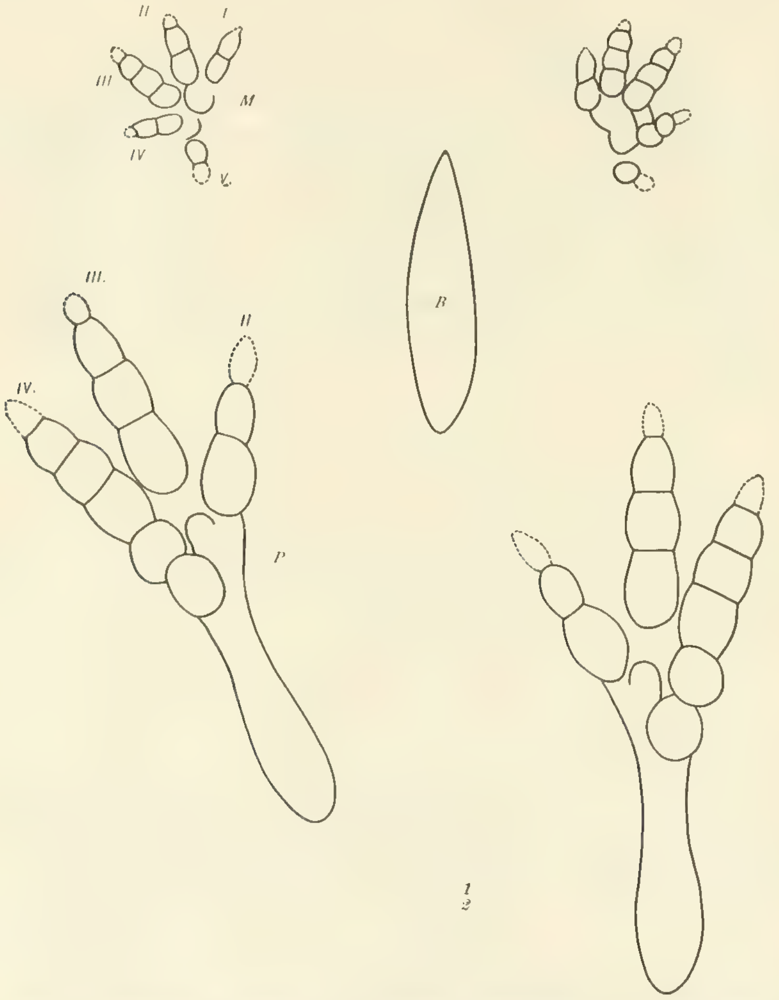


Fig 18. *Anomoepus scambus* E. Hitchcock. Impression of all four feet of a seated individual. × ½. B, impression of the breast; **M**, manus; P, pes. Drawn from no. $\frac{16}{5}$, of the Hitchcock cabinet. The manus is restored in outline after Deane.

Anomoepus scambus
E. Hitchcock.

Anomoepus scambus E. Hitchcock, **'48**, p. 222, pl. 13, fig. 1–6.

Anomoepus minor E. Hitchcock, **'58**, p. 57, pl. 9, fig. 1–2; pl. 34, fig. 2.

Specific characters. Pes: digit I, unknown. Divarication of digits II and III, 20° to 35°; of III and IV, 22° to 23°. Length of digit II, .049 to .057 m.; of III, .060 to .080 m.; of IV, .063 to .083 m. Length of foot, .095 m.; with the heel, .168 to .210 m.

Manus: divarication of digits I and II, 17.5° to 43°, a great variation, indicating a versatile pollex: of digits II and III, 22° to 29°; of III and IV, 24° to 50°; of IV and V, 55° to 87°; of I and V, 120° to 152°. Length of digit I, .024 m.; of II, .029 m.; of III, .032 m.; of IV, .024 m.; of V, .015 m. Length of step, .230 m. Width of trackway, .200 m.

Although it is the type species, *Anomoepus scambus* is of comparatively rare occurrence so that in the present memoir the morphological studies were made upon *A. intermedius*, perhaps the most abundant form. The figure (fig. 18) was studied from no. $\frac{16}{5}$, of the Hitchcock cabinet, together with no. $\frac{34}{40}$ and the drawing in Deane (**'61**, pl. 32). The last is from a magnificent specimen formerly owned by T. Leonard, Esq., of Greenfield, Massachusetts, and at present lost sight of. An interesting feature occurs on no. $\frac{34}{40}$, *viz.*, the somewhat lenticular impression of the breast of the animal possibly made by a plastron-like armature.

Types, nos. $\frac{16}{5}$ and $\frac{34}{40}$, of the Hitchcock cabinet, on red shale, the latter from Turner's Falls, Massachusetts.

Anomoepus intermedius E. Hitchcock.

Anomoepus intermedius E. Hitchcock, **'65**, pp. 2 and 7, pl. 1, fig. 1; pl. 15, fig. 1. This species is based upon part of *Brontozoum isodactylum* E. Hitchcock, **'58**, p. 69. Here also probably belong the following species: —

Sauropus barrattii E. Hitchcock, **'45b**, p. 24.

Aethiopus minor E. Hitchcock, **'58**, p. 69 (in part).

Plesiornis quadrupes E. Hitchcock, **'58**, p. 102, pl. 17, fig. 7; pl. 35, fig. 1–2; pl. 55, fig. 5.

Plectropterna minitans E. Hitchcock, **'58**, p. 108.

Apatichnus holyokensis C. H. Hitchcock, **'89b**, pp. 118, 123, 124.

Specific characters. Pes: divarication of digits I and II, 56°; of II and III, 20°; of III and IV, 35°; of I and IV, 110° or more. Length of digit II, .052 m.; of III, .073 m.; of IV, .057 m. Length of foot, .105 m.; including the heel, .173 m.

Manus: divarication of digits I and II, 33°; of II and III, 22°; of III and IV, 68°; of IV and V, but little, as they are nearly parallel. Length of digit I, .015 m.; of II, .028 m.; of III, .030 m.; of IV, .023 m. Length of step varies in the same animal from .140 to .235 m., the average being about .220 m. Width of trackway, .150 to .180 m.

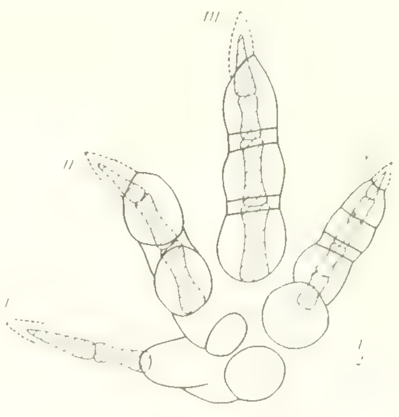


Fig. 19. *Anomoepus intermedius* E. Hitchcock. Impression of the right pes of a walking animal with the bones restored. × [illegible] From the type specimen, no. [illegible], of the Hitchcock cabinet.

This form differs from *A. scambus* in the greater divarication of the lateral digits and the greater relative stoutness of the foot in proportion to its length, and especially in the relatively shorter heel. An exceedingly interesting series of tracks is shown on slab no. $\frac{48}{1}$, of the Hitchcock cabinet, containing at least fifty impressions, all but four being of this species. Here the animal is shown walking, then stopping and sitting down, then rising and going on again. No caudal trace is exhibited until just before stopping, showing that ordinarily the tail was used as a counterpoise, only reaching the ground while the creature assumed the quadrupedal posture or just before. The impression of the ischial callosity is also to be seen. The difference in the character of the foot impression in the walking and sitting form is well shown and is brought out in figures 19 and 20, which are drawn from the slab in question.

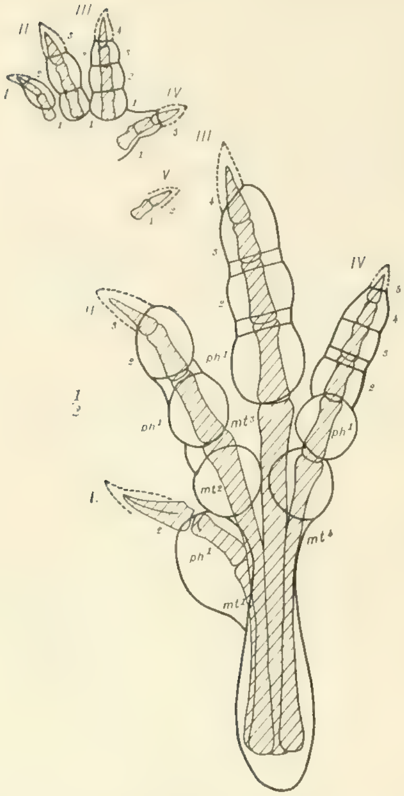


Fig. 20. *Anomoepus intermedius* E. Hitchcock. Tracks of the right manus and pes of a seated individual, probably identical with the one which made the track shown in figure 19. × ½. From the type slab, no. $\frac{48}{1}$, of the Hitchcock cabinet. The skeleton restoration shows the metatarsals and phalanges.

The type specimen is no. $\frac{48}{1}$ mentioned above, reddish sandstone from Turner's Falls, Massachusetts; figured in E. Hitchcock ('**65**, pl. 15, fig. 1). Figure 21 is from slabs nos. $\frac{54}{13}$ and $\frac{52}{4}$. The latter specimen C. H. Hitchcock recognizes as being *Apatichnus holyokensis* (*vide supra*).

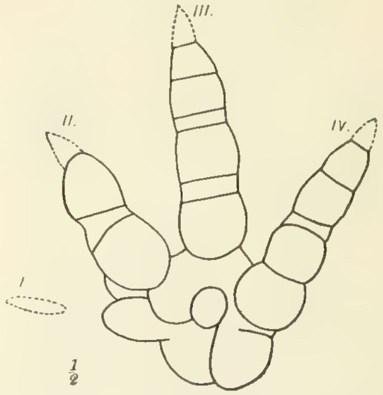


Fig. 21. *Anomoepus intermedius* E. Hitchcock. Impression of right pes. × ½. A composite drawing from nos. $\frac{54}{13}$ and $\frac{52}{4}$, of the Hitchcock cabinet.

Anomoepus curvatus E. Hitchcock.

Anomoepus curvatus E. Hitchcock, '**65**, p. 5, pl. 1, fig. 2; pl. 15, fig. 2.

Specific characters. Pes: divarication of digits I and II, 40°; of II and III, 23.5°; of III and IV, 36.5°. Length of digit II, .050 m.; of III, .064 m.; of IV, exclusive of sole pad, .055 m. Length of foot, .098 m. The heel and manus are unknown. Length of step, .230 to .250 m.

The species *curvatus* approximates *intermedius* very closely, being distinguished chiefly by its smaller size, by the lesser divergence of the outer toe, and by the distinct inward curvature of the middle toe which is present, though to a less degree, in the fourth toe.

The type specimen is no. $\frac{52}{10}$, of the Hitchcock cabinet, a photograph of which may be seen in E. Hitchcock (**'65**, pl. 15, fig. 2). This specimen is from Lily pond, at Turner's Falls, Massachusetts (fig. 22).

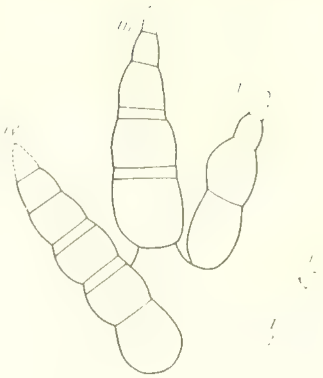


Fig. 22. *Anomoepus curvatus* E. Hitchcock. Imprint of left pes. × ½. From the type specimen, no. $\frac{52}{10}$, of the Hitchcock cabinet.

Anomoepus crassus (C. H. Hitchcock).

Apatichnus crassus C. H. Hitchcock, **'89b**, pp. 118, 122, 124.

Specific characters. Pes: divarication of digits I and II, 80°; of II and III, 32°; of III and IV, 40°; of II and IV, 72°. Length of digit II, .085 m.; of III, .102 m.; of IV, not including the sole pad, .083 m.; including the sole pad, .120 m. Length of foot, .190 m. Distance between lateral tips, .140 m. Length of step, .387 m.

Manus: width of impression, .060 m.; length, .060 m.

The foot of *A. crassus* resembles that of *A. intermedius* in general form but is considerably larger and the hallux is rotated backward to a greater extent than in the latter form. *A. crassus* is reported only from New Jersey, the type specimen, which is preserved in the museum of Rutgers college, being from Whitehall, near Boonton, in that state (fig. 23).

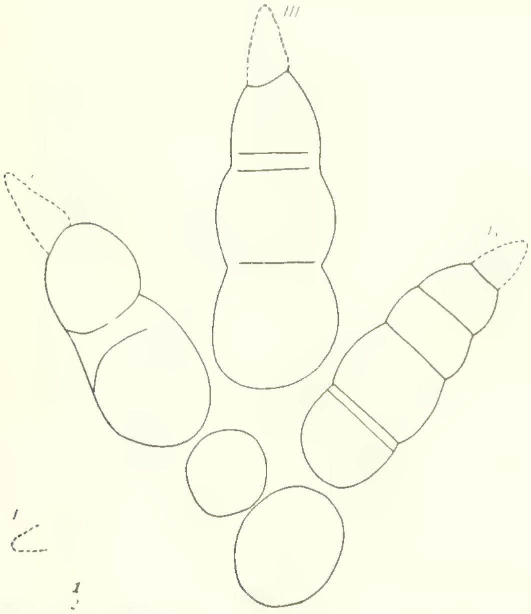


Fig. 23. *Anomoepus crassus* C. H. Hitchcock. Impression of right pes. × ⅓. From the type specimen in the museum of Rutgers college.

Anomoepus minimus E. Hitchcock.

Anomoepus minimus E. Hitchcock, **'65**, p. 5, pl. 2, fig. 2.

Specific characters. Pes: divarication of digits II and III, 40°; of III and IV, 35°. The hallux does not appear on the type specimen. The length of digit II is .035 m.; of III, .050 m.; of IV, .033 m. Length of foot, .054 m. Heel unknown.

Manus: divarication of digits I and II, 40°; of II and III, 25°; of III and IV, 48°; of IV and V, 28°. Length of digit I, .012 m.; of II, .014 m.; of III, .021 m.; of IV, .014 m.; of V, .010 m. Length of step, .170 to .210 m. Width of trackway, .076 m.

This species is readily distinguishable from all but the next succeeding species, by its small size and delicate proportions.

The type is no. $\frac{55}{112}$, of the Hitchcock cabinet, from Gill, Massachusetts, and is here shown (fig. 24).

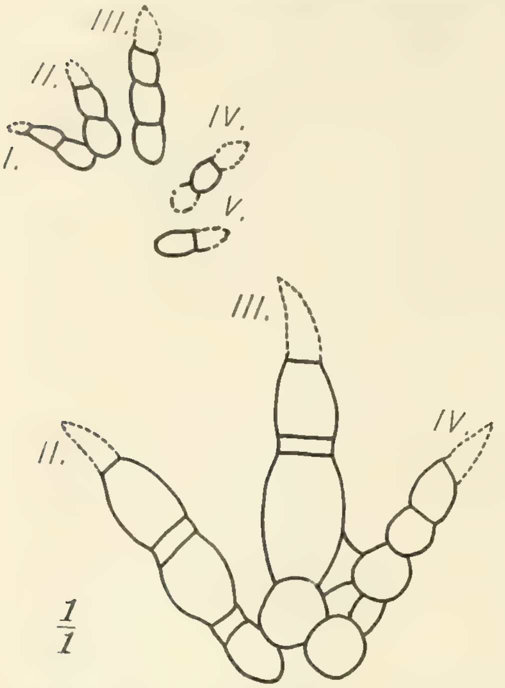


Fig. 24. *Anomoepus minimus* E. Hitchcock. Impressions of the right manus and pes. × 1/1. A composite figure from the type specimen, no. $\frac{55}{112}$ and no. [illegible] of the Hitchcock cabinet.

Anomoepus gracillimus (E. Hitchcock).

Eubrontes gracillimus E. Hitchcock, **'45b**, p. 23.

Brontozoum gracillimum E. Hitchcock, **'48**, p. 175.

Grallator gracillimus E. Hitchcock, **'58**, p. 73, pl. 13, fig. 5; pl. 39, fig. 2.

Anomoepus gracillimus C. H. Hitchcock, in E. Hitchcock, **'65**, p. 6.

Specific characters. Pes: divarication of digits II and III, 28°; of III and IV, 23°. Length of digit II, .039 m.; of III, .050 m.; of IV, .046 m. Length of foot, .064 m. Length of step, .180 to .200 m. Width of trackway, .090 m.

This form was removed from Grallator by C. H. Hitchcock, with the acquiescence of his father, on the following grounds: "First, the short stride of the animal; second, the thick, Anomoepus type of the foot; and third, the occasional presence of a long heel upon the hind foot." It differs from *A. minimus* chiefly in the much less divarication of the toes.

The type is no. $\frac{50}{1}$, of the Hitchcock cabinet, on red sandstone from Turner's Falls, Massachusetts.

Anomoepus cuneatus C. H. Hitchcock.

Anomoepus cuneatus C. H. Hitchcock, **'89b**, pp. 118, 125.

Specific characters. Pes: divarication of digits II and IV, 40°. Length of step, .330 to .460 m. Width of trackway, .178 m. "Long and distinct impression made by the middle toe and also by a slender tail. Like *Grallator cuneatus*. Shorter stride and length of step would seem to ally it with Anomoepus." These reasons, as given by Hitchcock, are valid as far as they go, but further study seems necessary to decide without question the true position of this form.

The type specimen is no. 105 of the Mt. Holyoke museum.

Anomoepus isodactylus C. H. Hitchcock.

Anomoepus isodactylus C. H. Hitchcock, **'89b**, pp. 118, 124.

Specific characters. Pes: divarication of digits I and II, 50°; of II and III, 29°; of III and IV, 30°. Length of hallux, .043 m.; of digit II, .043 m.; of III, .072 m.; of IV, including the sole pad, .101 m. Average width of phalanges, .025 m. Length of foot, .115 m.; including the heel, .230 m. The basal pads of the hallux, as well as the claw, impress, showing that toe to be incumbent. Manus: unknown. Length of step, .205 m.

This species is based upon specimens in the Mt. Holyoke museum, but of the specimens labeled *A. isodactylus*, one is clearly *A. intermedius*, while the others, no. 128 and its counterpart no. 142, are the ones used for this description, the figure (fig. 25) being drawn from the former. Another slab in the northeast corner of the museum, and bearing no number, has the impression of the sitting animal of this species. This form resembles somewhat superficially *A. intermedius*, but is a heavier, broader toed animal, with a foot very short in proportion to its width.

Type specimens, nos. 128 and 142, of the Mt. Holyoke museum, from South Hadley, Massachusetts.

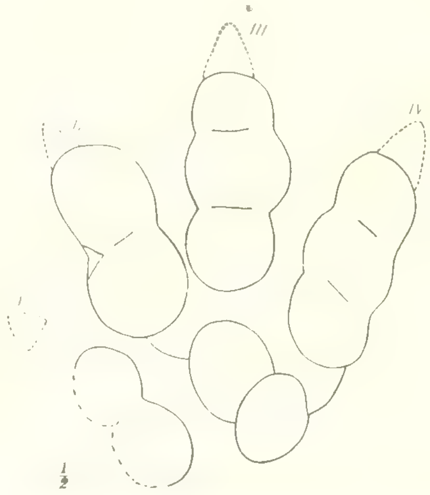


Fig. 25. *Anomoepus isodactylus* C. H. Hitchcock. Imprint of the right pes × ½. From the type specimen, no. 126, of the Mt. Holyoke college collection.

Genus **Fulicopus** E. Hitchcock. (Fulica foot.)

Fulicopus E. Hitchcock, **'45b**, p. 23.
Anomoepus E. Hitchcock, **'58**, p. 56 (in part).

Generic characters. The members of this genus are distinguished from Anomoepus by the greater size, especially of the pes, less acuminate claws, and the absence of the sole pad in addition to the four normally belonging to digit IV. An ischial callosity may also be present. The track of the pes shows less divarication of the toes than does that of Anomoepus and in general appearance resembles

Eubrontes very closely. It is distinguished from Eubrontes, however, by the presence of the heel and the partly rotated hallux. When the animal is walking and these two characters are not seen it is very difficult to distinguish the two genera.

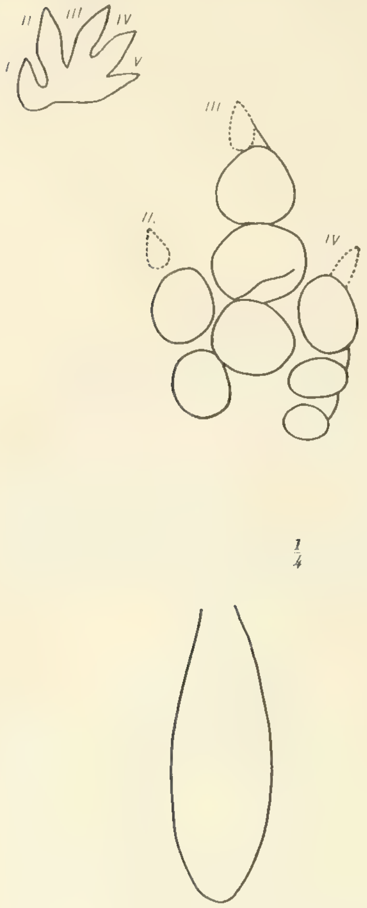


Fig. 26. *Fulicopus lyellianus* E. Hitchcock. Impressions of the right manus and pes of a seated individual. × ¼. From the type specimen (*Anomoepus major*), no. $\frac{1}{1}$, of the Hitchcock cabinet.

Fulicopus lyellianus E. Hitchcock.

Fulicopus lyellianus E. Hitchcock, **'45b**, p. 23.
Aethyopus lyellianus E. Hitchcock, **'48**, p. 178.
Anomoepus major E. Hitchcock, **'58**, p. 56, pl. 8.
Amblonyx lyellianus E. Hitchcock, **'58**, p. 71, pl. 13, fig. 2; pl. 37, fig. 2.

Specific characters. Pes: divarication of digits I and II, 40°; of II and III, 11.5°; of III and IV, 14°. Length of digit I, .083 m.; of II, .103 m.; of III, .147 m.; of IV, .156 m. Length of foot, .220 m.; of foot and heel, .427 m. Breadth of heel, .050 m. Distance between lateral tips, .110 m.

Manus: divarication of digits I and II, 6°; of II and III, 32°; of III and IV, 20°; of IV and V, 26°. Length of digit I, .031 m.; of II, .038 m.; of III, .040 m.; of IV, .033 m.; of V, .020 m. Length of step, .765 m. Width of trackway, .127 m. Length of ischial callosity, .055 m.; width, .060 m.

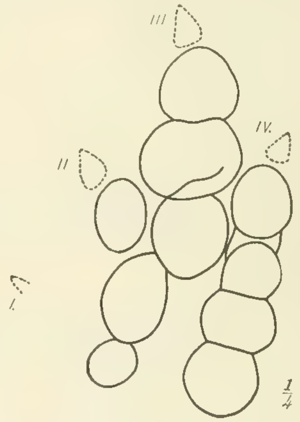


Fig. 27. *Fulicopus lyellianus* E. Hitchcock. Imprint of the right pes of a walking individual, identical with the one that made the impressions shown in figure 28. × ¼. From the type track, on slab no. $\frac{1}{1}$, of the Hitchcock cabinet.

The posture of the animal is somewhat different from that of Anomoepus for here the creature brings the hind limbs more under the body so that very little weight is borne on the hands as in the kangaroo. This makes a very light and incomplete manus impression, no pads being discernible. The claws are more slender in proportion to the width of the fingers than in Anomoepus, probably correlated with their slight use as supporting organs and consequent greater prehensile function.

The type specimens of *Fulicopus lyellianus*, nos. $\frac{1}{1}$ and $\frac{31}{85}$, of the Hitchcock cabinet, are referable to *Anomoepus major*, being identical in form and size with the latter after allowing for such changes as the shifting of the animal's weight from the heel to the whole foot while walking, would make, especially in the posterior pads. The specimen of *F. lyellianus* on slab no. $\frac{1}{1}$ on which the type of *A. major* is also found, is so similar to the latter as to lead to the belief that they were made by the same individual. This belief is increased by the occurrence of certain unique markings upon both tracks which are brought out in the figures. This seems to prove the synonymy of the two species (compare figures 26 and 27). *Fulicopus lyellianus* as a name should have priority and must be used though the generic name was founded upon a misconception. The other species of the genus, *Fulicopus giganteus*, is referred to Eubrontes under the specific name *platypus* as there is a *giganteus* already in the genus.

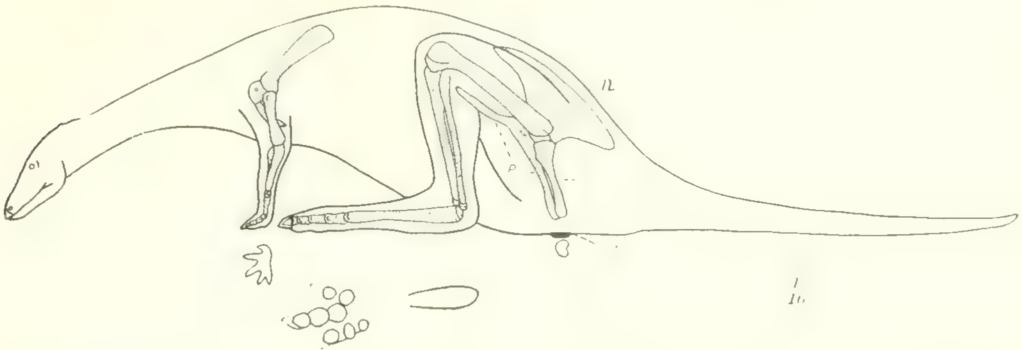


Fig. 28 *Fulicopus lyellianus* E. Hitchcock. Restoration of the dinosaur in the attitude of feeding. × $\frac{1}{16}$. Based upon the footprints figured above (fig. 26). The general contour and the bones are suggested by Marsh's figured restoration of Hypsilophodon, although the proportions of the limb segments are altered. The lateral digits of manus and pes are omitted for clearness. Il., ilium; Is., ischial bones; Is. C., ischial callosity; Pu., pubic bones.

The peculiar heart-shaped impression shown in figure 28 (see also E. Hitchcock, **'65**, pl. 19) behind and between the heels, already alluded to as that of the ischial callosity, is attributed by E. Hitchcock (**'58**, p. 56) to the end of a truncated tail. The paired ends of the ischial bones upon which the Orthopoda rested, would come at just about the position indicated by the mark in question, and while the bones themselves could not have made the impression, a callosity such as the sternal callosity seen in the dromedary, is not out of the question and seems the most likely explanation that can be given.[1] Figure 28 attempts to show the animal seated as though drinking and demonstrates this idea.

In the type specimen of *Anomoepus intermedius*, no. $\frac{48}{1}$, of the Hitchcock cabinet, impressions both of the tail and of the ischial callosity of the same individual may be seen, the difference in the two marks being such that they could not have been made by the same organ, the former being a narrow groove while the latter is a broad rounded depression.

---

[1] The possibility of a callosity being present was suggested to the author by Mr. Charles R. Knight, though the conception of the posture together with the restoration are the writer's own.

The type specimens are nos. $\frac{1}{1}$ and $\frac{1}{7}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Genus **Apatichnus** E. Hitchcock. (Deceptive track.)

Apatichnus E. Hitchcock, **'58**, p. 99.

Generic characters. Bipedal in gait, digitigrade, functionally tridactyl. Claws on the pes are acuminate and the proximal pad of digit IV is very small. There is a caudal trace.

The distinction between this genus and Anomoepus was supposed to be the presence of a hallux in the present group and its absence in the other. It has been found in both genera thus removing several of the species from Apatichnus to Anomoepus as they were clearly of the latter type but were known to possess the hallux.

Apatichnus, of which *A. circumagens* is the type, differs from Anomoepus in the much shorter hallux and in the fact that, while the divarication between digits II and III is less, that between III and IV is much greater, giving to the middle digit the appearance of being exserted far beyond the others, a point which is well brought out in the figures.

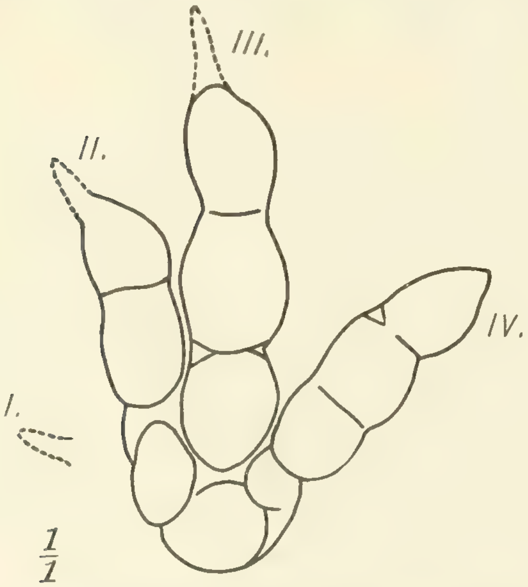


Fig. 29. *Apatichnus circumagens* E. Hitchcock. Impression of right pes. × $\frac{1}{1}$. From no. $\frac{23}{8}$, of the Hitchcock cabinet.

Apatichnus circumagens E. Hitchcock.

Apatichnus circumagens E. Hitchcock, **'58**, p. 100, pl. 17, fig. 5; pl. 35, fig. 6.

Specific characters. Pes: divarication of digits I and II, 53°; of II and III, 18°; of III and IV, 46°; of I and IV, 116°. Length of digit I, .025 m.; of II, .035 m.; of III, .062 m.; of IV, .053 m. Length of foot, .075 m. These measurements are taken from no. $\frac{23}{8}$, the figured specimen; those of Hitchcock, from no. $\frac{21}{2}$, are somewhat larger and the angle of divarication of digits II and III is greater. Hitchcock gives the length of the entire foot and heel as .127 m., the foot alone being half that length. The average length of step is .240 m.

Manus: turned inward toward the median line. Caudal trace sinuous, not always present.

Type specimen, no. $\frac{21}{2}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts. Figured specimen, no. $\frac{23}{2}$, on red micaceous sandstone from the Ferry at Turner's Falls, Massachusetts (fig. 29).

Apatichnus minus (E. Hitchcock).

Gigantitherium minus E. Hitchcock, **'58**, p. 95, pl. 17, fig. 1; pl. 41, fig. 2; pl. 42, fig. 2.

Specific characters. Pes: divarication of digits II and III, 20°; of III and IV, 43.5°. Length of digit II, .108 m.; of III, .147 m.; of IV, .146 m. Length of foot, .225 m. Distance between lateral tips, .160 m. Length of step, .630 m. Width of trackway, .167 m. Caudal trace straight, interrupted at each step. Manus: unknown.

This form was associated by Hitchcock with *Gigandipus caudatus*, though a far smaller species, but its affinities seem to be rather with Apatichnus, as it is evidently of the same type as *A. circumagens* (compare figures 29 and 30).

Type specimen, no. $\frac{1}{3}$, of the Hitchcock cabinet, on micaceous shale from Lily pond, Turner's Falls, Massachusetts (fig. 30).

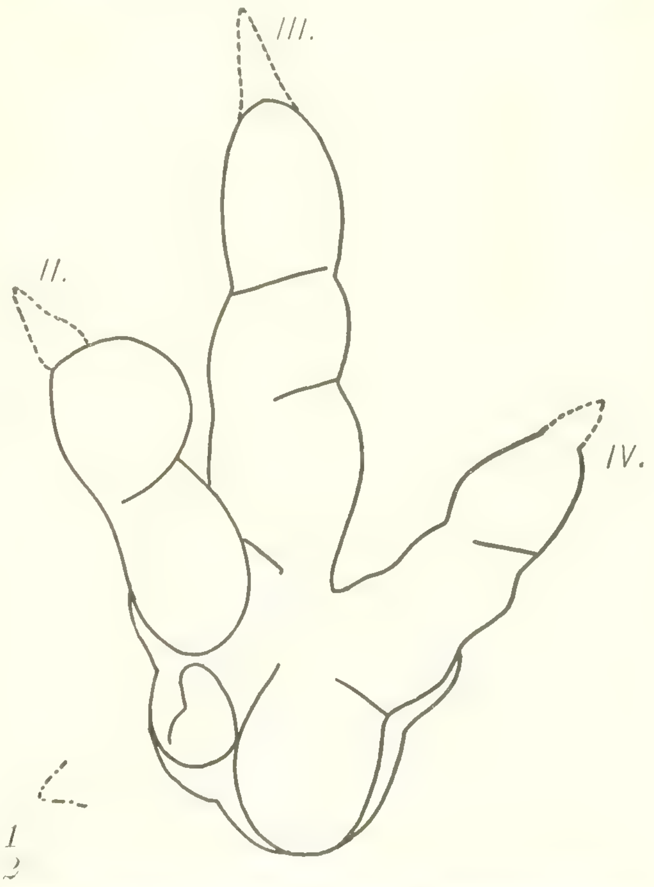


Fig. 30. *Apatichnus minus* E. Hitchcock. Imprint of the right pes × ½. From the type specimen, no. $\frac{1}{3}$, of the Hitchcock cabinet.

Genus **Corvipes** E. Hitchcock. (Crow foot.)

Corvipes E. Hitchcock, **'58**, p. 98.

Generic characters. Quadrupedal. Pes tridactylous, ornithoid, digitigrade. Manus pentadactylous, digits curved, position of print a little in advance of, sometimes without, again covered in part by that of the pes. No phalangeal nor claw impressions. Tips of digits more or less acuminate.

Corvipes lacertoideus E. Hitchcock.

Corvipes lacertoideus E. Hitchcock, **'58**, p. 98, pl. 17, fig. 3; pl. 47, fig. 1; pl. 35, fig. 7.

Specific characters. Pes: divarication of digits II and III, 40°; of III and IV, 35°; of II and IV, 75°. Length of digit II, .033 m.; of III, .043 m.; of IV, .033 m. Length of heel, .023 m.; of the foot, .066 m. Length of step, .043 to .068 m.

Manus: divarication of digits I and V, 160°. Length of digit I, .010 m.; of II, .010 m.; of III, .019 m.; of IV, .020 m.; of V, .015 m.; of the hand, .033 m.

Type specimen, no. $^{32}_{1}$, of the Hitchcock cabinet, on sandstone, from Turner's Falls, Massachusetts.

Family **EUBRONTIDAE**.

Family characters. Large bipedal forms, more or less rounded claws, digits broad with distinct phalangeal pads. Foot functionally, possibly structurally tridactyl as the hallux claw never impresses. No caudal trace.

Genus **Eubrontes** E. Hitchcock.

Eubrontes E. Hitchcock, **'45b**, p. 23.

Brontozoum E. Hitchcock, **'47**, p. 50.

Generic characters are those of the family. This genus is distinguished from Anchisauripus by the greater size, generally broader digits, and blunter claws, and by the absence of the hallux. A possible exception to the last point is seen in specimen no. $^{15}_{1}$, of *E. giganteus*, from Northampton, Massachusetts, which is so deep that it will hold a gallon of water. This shows what seems to be the impression of a hallux claw in the same position to the rear as in the genus Anchisauripus, but the claw instead of being a prehensile one is more of the character of the anterior claws.

E. giganteus is the type species.

Eubrontes giganteus E. Hitchcock.

Eubrontes giganteus E. Hitchcock, **'45b**, p. 23.

Brontozoum giganteum E. Hitchcock, **'47**, p. 57; **'58**, p. 64, pl. 33, fig. 1–3; pl. 41, fig. 1; pl. 53, fig. 7; pl. 57, fig. 1.

Recharacterized by C. H. Hitchcock, in E. Hitchcock, **'65**, p. 23, pl. 10, fig. 1.

Specific characters. Divarication of digits II and III, 18°; of III and IV, 20°.

Length of digit II, .200 m.; of III, .260 m.; of IV, .285 m. Distance between lateral claws, .225 m. Length of foot, .370 m. Length of step, 1.090 to 1.170 m.

This form is the largest of the genus and with the possible exception of *Otozoum moodii* and *Gigandipus caudatus*, the largest of all the Connecticut valley dinosaurs. The track would indicate an animal eighteen to twenty feet in length and of massive build. Its occurrence is among the most frequent and it has been reported from Massachusetts, Connecticut, and New Jersey.

The type is no. $\frac{45}{8}$, of the Hitchcock cabinet, locality unrecorded. The figure (fig. 31) is drawn from no. $\frac{45}{1}$ of the same collection.

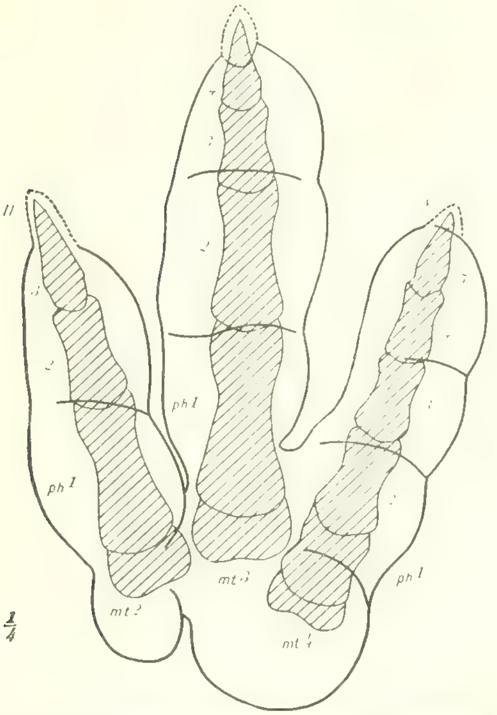


Fig. 31. *Eubrontes giganteus* E. Hitchcock. Impression of the right pes, with the skeleton of the foot restored. × $\frac{1}{4}$. From no. $\frac{45}{1}$, of the Hitchcock cabinet.

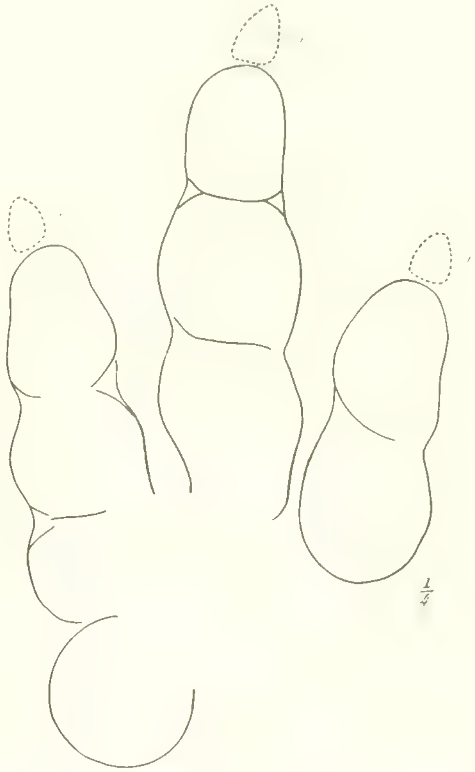


Fig. 32. *Eubrontes approximatus* (C. H. Hitchcock). Imprint of the left pes. × $\frac{1}{4}$. From no. $\frac{8}{1}$, of the Hitchcock cabinet.

Eubrontes approximatus (C. H. Hitchcock).

Brontozoum approximatum C. H. Hitchcock, in E. Hitchcock, **'65**, p. 23, pl. 10, fig. 2.

Specific characters. Divarication of digits II and III, 15° to 30°; of III and IV, 13° to 24°. Length of digit II, .192 to .153 m.; of III, .274 to .230 m.; of IV, .308 to .295 m. Length of foot, .408 to .381 m. Length of step from no. $\frac{8}{1}$, .910 to 1.080 m. In the above measurements the first given is from the figured specimen, no. $\frac{32}{51}$, the second from the type, no. $\frac{54}{10}$, of the Hitchcock cabinet.

This form is very near *E. giganteus* being distinguished therefrom mainly by its more slender proportions. The other distinguishing feature mentioned by C. H. Hitchcock, namely, that of the greater divarication of the toes, is not always apparent as the measurements show. The digits average .045 to .075 m. in width for *approximatus* as contrasted with .080 to .100 m. for *giganteus*.

Type, no. $\frac{54}{10}$, of the Hitchcock cabinet, on gray shale from Turner's Falls, Massachusetts. It is also reported from Connecticut and New Jersey (fig. 32).

Eubrontes divaricatus (E. Hitchcock).

Brontozoum divaricatum E. Hitchcock, **'65**, p. 7, pl. 4, fig. 1.

Specific characters. Divarication of digits II and III, 20°; of III and IV, 35° to 50°. Length of digit II, .193 m.; of III, .243 m.; of IV, .262 m. Length of foot, .340 to .360 m. Length of step, 1.040 to 1.190 m.

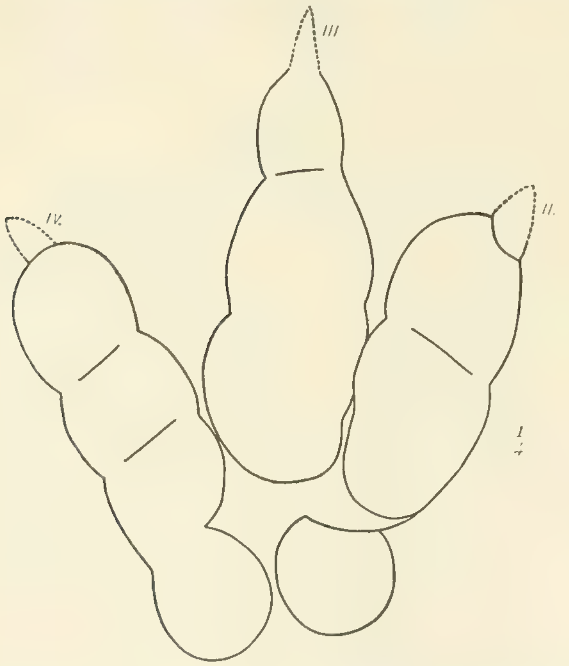


Fig. 33. *Eubrontes divaricatus* (E. Hitchcock). Impress of the left pes. × $\frac{1}{4}$. Drawn from the type specimen, no. $\frac{58}{1}$, of the Hitchcock cabinet.

E. divaricatus is best shown in the type specimen, no. $\frac{58}{1}$ (fig. 33), which contains a row of four very deep tracks. It is distinguished, apart from size, by the decided divarication of the outer toe, a readily recognizable feature. In size it lies between *E. giganteus* on the one hand and *E. platypus* on the other.

The type, no. $\frac{58}{1}$, of the Hitchcock cabinet, is on hard shale, the locality being unrecorded.

Eubrontes platypus nom. nov.

Amblonyx giganteus E. Hitchcock, **'58**, p. 71, pl. 13, fig. 1; pl. 38, fig. 1–2; pl. 57, fig. 5.

Specific characters. Divarication of digits II and III, 12°; of III and IV, 22°. Length of digit II, .157 m.; of III, .190 m.; of IV, .215 m. Distance between lateral claws, .190 m. Length of foot, .267 m. Length of step, 1.135 m. Very long limbed.

This species is revived although dropped by E. Hitchcock (**'65**, p. 2). The resemblance between it and *Anchisauripus tuberatus* is very close as regards size and general conformation, except that in the present species the phalangeal pads especially in the middle and outer digits, are much broader and the claws of all three toes are broad and blunted in contrast to the long, acuminate claw in *A. tuberatus*. The change of name was necessitated by the fact that the specific name *giganteus* was preoccupied in the genus.

Type, no. $\frac{13}{4}$, of the Hitchcock cabinet; red shale from Turner's Falls, Massachusetts (fig. 34).

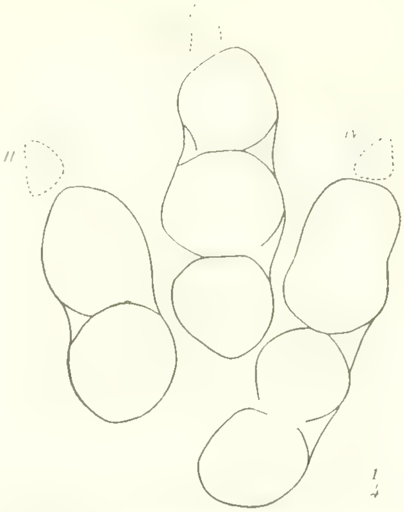


Fig. 34. *Eubrontes platypus* Lull. Imprint of the right pes. × $\frac{1}{4}$. From the type specimen, no. $\frac{13}{4}$, of the Hitchcock cabinet.

Family **OTOZOIDAE**.

With the characters of the genus Otozoum.

Genus **Otozoum** E. Hitchcock. (Giant animal.)

Otozoum E. Hitchcock, **'47**, p. 54.

Generic characters. Large tracks, that of the pes being more than twice the length of the manus. Pes plantigrade, tetradactyl, all of the digits pointing forward. Digits broad with well marked phalangeal pads; claws rounded. The foot has a broad web-like flange extending beyond the tips of the toes, whose probable function was to support the animal in soft mud, possibly, however, for swimming. Manus pentadactyl. Phalangeal formula: (?) 2. 3. 3. 3. 3; digits III, IV, and V, clawed, fingers half webbed. This manus, if the interpretation be correct, is unique for a dinosaur and subsequent study may remove Otozoum from the order.

Otozoum moodii E. Hitchcock.

Otozoum moodii E. Hitchcock, **'47**, p. 55, fig. 1; **'58**, p. 123, pl. 22; pl. 23, fig. 1; pl. 33, fig. 4–5; pl. 46, fig. 5.

Specific characters. Pes: divarication of digits I and II, 25°; of II and III, 4°; of III and IV, 11°. Length of digit I, .196 m.; of II, .230 m.; of III, .192 m.; of IV, .202 m. Length of foot, .490 m.; to extremity of web, .534 m. Breadth of foot across web, .400 m.; distance between lateral tips, .380 m. (pl. 72, fig. F–G).

Manus: divarication of digits I and II, 53°; of II and III, 40°; of III and IV, 36.5°;

of IV and V, 40°. Length of digit I, .056 m.; of II, .080 m.; of III, .092 m.; of IV, .098 m.; of V, .090 m. Length of foot, .206 m. (pl. 72, fig. E). Length of step, about .800 m.

The type specimen is no. $\frac{5}{14}$, of the Hitchcock cabinet, in high relief on coarse sandstone from South Hadley, Massachusetts. The counterpart, no. $\frac{3}{1}$, is taken some distance below the surface on which the animal walked as the layer of red mud which intervened was incapable of preservation.

The studies of the bone restoration of the pes are largely conventional and the results represent the most generalized dinosaurian foot which would be likely to be found in a bipedal dinosaur. The fifth digit is represented as vestigial. An accurate restoration of the manus skeleton will need the elucidation of further material. The genus Otozoum shows some extremely interesting parallelisms with the Stegocephalian genus Chirotherium which would lead one to suspect an actual relationship were it not for the fact that the phalangeal formula of the earlier form is such that that of Otozoum could never have been derived from it. The parallelisms and contrasts are: —

Chirotherium (pl. 72, fig. A–D).	**Otozoum** (pl. 72, fig. E–G).
Quadrupedal.	Bipedal.
Pes pentadactyl.	Pes tetradactyl.
Pads well developed.	Pads well developed.
Plantigrade.	Plantigrade.
Claws rounded.	Claws rounded.
Web extending beyond the toes.	Web extending beyond the toes.
Phalangeal formula: 2. 3. 4. *4*. 2.	Phalangeal formula: 2. 3. 4. *5*. 0.
Manus pentadactyl.	Manus pentadactyl.
Claws reduced.	Claws on II, III, and IV, developed.
Web as in pes.	Web reduced.
Phalangeal formula: 2. 3. 3. 3. 3.	Phalangeal formula: 2. 3. 3. 3. 3.
Hand pointing forward.	Hand turned inward.
Habits apparently similar as the preservation of the tracks is the same in each instance. Relative length of the foot to the stride is the same.	
Lower and upper Trias.	Jura-Trias.
C. barthii. C. storetonensis.	*O. moodii.*

Otozoum caudatum C. H. Hitchcock.

Otozoum caudatum C. H. Hitchcock, **'71**, p. xxi; **'89b**, pp. 119, 127.

The present author seriously questions the validity of this species, which is distinguished from *O. moodii* only by the presence of a tail trace which could readily occur in

O. moodii provided the specimens showed the animal's track under favorable circumstances, that is, just before stopping. The other character, that of a forwardly directed "thumb" (hallux) as against a recurved one in *O. moodii* is hardly a valid distinction for the reason that the curvature is not a constant character, in fact it is of rare occurrence.

The type specimen of this species, if such it is, is in the museum of Wesleyan university, at Middletown, Connecticut.

? **Otozoum parvum** C. H. Hitchcock.

Otozoum parvum C. H. Hitchcock, **'89b**. pp. 119, 122, 127.

Specific characters. Pes: divarication of digits I and II, 24°; of II and III, 16°; of III and IV, 14°; of I and IV, 54°. Length of digit I, .076 m.; of II, .120 m.; of III, .128 m.; of IV, .102 m. Length of foot, .190 m. On one slab from Milford, New Jersey, preserved in the Geological museum, at Lafayette college, a fifth digit, arising near the base of the fourth, is seen, very similar indeed to Chirotherium.

Manus: divarication of digits I and II, 29°; of II and III, 16°; of III and IV, 40°; of IV and V, 14°. Length of digit I, .030 m.; of II, .034 m.; of III, .035 m.; of IV, .025 m.; of V, .020 m. Length of entire impression, .075 m.

This form is not Otozoum; in fact it suggests Chirotherium much more strongly, and further study may prove the identity of this species with the latter.

The type specimen is preserved in the museum of Lafayette college, Easton, Pennsylvania.

Order *INCERTAE SEDIS.*

Forms habitually bipedal.

Genus **Platypterna** E. Hitchcock. (Broad heel.)

Platypterna E. Hitchcock, **'45b**, p. 25; **'58**, p. 83.

Generic characters. Bipedal, tridactyl, plantigrade or digitigrade, generally with a broad, rounded heel. Digits narrow, without pad impressions and but rarely showing distinct claws.

This is one of the "leptodactylous" genera whose characters it is very difficult to make out. It would seem best to place it provisionally with the carnivorous dinosaurs because of the bipedal gait and dinosauroid character of the foot.

Platypterna deaniana E. Hitchcock.

Platypterna deanianus E. Hitchcock, **'45b**, p. 25; **'58**, p. 83, pl. 14, fig. 4.

Specific characters. Pes: divarication of digits II and III, 40° to 45°; of III and IV, 25° to 30°; of II and IV, 60° to 70°. Length of digit II, .038 m.; of III, .076 m.; of IV, .051 m. Heel: length, .030 m.; breadth, .023 m. Distance between lateral tips, .051 to .063 m. Length of foot, .100 to .115 m.

E. Hitchcock (**'65**, p. 2) speaks of this form as of doubtful validity, possibly because of its probable identity with *Sillimanius tetradactylus*.

The type specimen is no. $\frac{32}{26}$, of the Hitchcock cabinet, on fine red shale from Weathersfield, Connecticut.

Platypterna concamerata (E. Hitchcock).

Harpedactylus concameratus E. Hitchcock, **'48**, p. 207, pl. 14, fig. 3.
Platypterna varica E. Hitchcock, **'58**, p. 85, pl. 14, fig. 8; pl. 47, fig. 4.

Specific characters. Pes: divarication of digits II and III, 23°; of III and IV, 52°; of II and IV, 75°. Length of digit II, measured from the middle of the heel, .076 m.; of III, .091 m.; of IV, .051 m.; of the heel, .028 m. Width of heel, .050 m. Length of foot, .127 m. Distance between lateral tips, .094 m. Length of step, .200 to .300 m. Width of trackway, .280 m.

This form is peculiar in the size and breadth of the heel and the curvature of the toes. It is also remarkable for the extreme width of the trackway as the specific name implies.

The type specimen is no. $\frac{11}{1}$, of the Hitchcock cabinet, on gray micaceous sandstone from Turner's Falls, Massachusetts.

Platypterna digitigrada E. Hitchcock.

Platypterna digitigrada E. Hitchcock, **'58**, p. 86, pl. 14, fig. 9; pl. 51, fig. 2.

Specific characters. Pes: divarication of digits II and III, 43°; of III and IV, 37°; of II and IV, 80°. Length of digit II, .020 m.; of III, .030 m.; of IV, .023 m. Distance between lateral tips, .040 m. Length of foot, .050 m.; width of heel, .020 m. Length of step, .100 to .115 m. Width of trackway, .076 m. Toes curving inwards; thick, with acuminate claws.

This track is analogous to that of *Platypterna gracillima*, that is, a further caving of the mud in the present instance would readily produce the latter, though no real clue to its identity with any other genus is shown.

The type specimen is no. $\frac{36}{16}$, of the Hitchcock cabinet, on shale from Turner's Falls, Massachusetts.

? **Platypterna gracillima** E. Hitchcock.

Platypterna gracillima E. Hitchcock, **'58**, p. 86, pl. 14, fig. 12.

Specific characters. Pes: divarication of digits II and III, 20°; of III and IV, 50°; of II and IV, 70°. Length of digit II, .025 m.; of III, .038 m.; of IV, .032 m. Distance between lateral tips, .036 m. Length of step, .127 to .140 m. Width of trackway, .076 m. Foot digitigrade, outer toes curved inward.

This track is like that of a miniature of *Argoides redfieldianus*, which is probably to be identified with *Eubrontes divaricatus*. The foot approximates most nearly that of *Grallator gracilis*; but the angles of divarication are far greater in the present form. The species is evidently not of the genus Platypterna but is left therein provisionally until further light is had upon its affinities.

The type is no. $\frac{39}{4}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Platypterna tenuis E. Hitchcock.

Platypterna tenuis E. Hitchcock **'45b**, p. 25; **'58**, p. 84, pl. 14, fig. 5; pl. 58, fig. 10.

Specific characters. Pes: divarication of digits II and III, 20° to 30°; of III and IV, 25° to 30°; of II and IV, 45° to 60°. Length of digit II, .025 m.; of III, .042 m.; of IV, .035 m. Breadth of heel, .015 m. Distance between lateral tips, .048 m. Length of foot, .069 m. Length of step, .178 m. Width of trackway, .050 m.

The form is semiplantigrade so that the whole foot does not impress; a long limbed, delicate type.

The type specimen is no. $\frac{32}{38}$, of the Hitchcock cabinet, on red shale from Weathersfield, Connecticut.

Platypterna delicatula (E. Hitchcock).

Calopus delicatulus E. Hitchcock, **'45b**, p. 25.

Platypterna delicatula E. Hitchcock, **'58**, p. 84, pl. 14, fig. 6; pl. 58, fig. 8.

Specific characters. Pes: divarication of digits II and III, 22°; of III and IV, 18°; of II and IV, 40°. Length of digit II, .017 m.; of III, .028 m.; of IV, .019 m.; of the heel, .010 m. Width of heel, .008 m. Distance between lateral tips, .015 m. Length of step, .076 m. Width of trackway, .050 m.

This is the smallest representative of the genus.

Type specimen, no. $^{31}_{11}$, in the Hitchcock cabinet, on red shale from Weathersfield, Connecticut.

Platypterna recta (E. Hitchcock).

Harpedactylus rectus E. Hitchcock, **'48**, p. 209, pl. 5, fig. 5; pl. 24, fig. 7.

Platypterna recta E. Hitchcock, **'58**, p. 84, pl. 14, fig. 7; pl. 47, fig. 3.

Specific characters. Pes: divarication of digits II and III, 10°; of III and IV, 27°; of II and IV, 36°. Length of digit II, .055 m.; of III, .080 m.; of IV, .060 m. Distance between the lateral tips, .063 m. Length of track, .095 m. Width of heel, .045 m. Length of step, .140 m. Width of trackway, .140 m.

In this form, as in *P. tenuis*, the foot is semiplantigrade so that the entire foot does not impress. The toes are straight but the short step and wide trackway indicate a very short limbed, wide bodied form as in the case of *P. concamerata.*

The type is no. $^{6}_{2}$, of the Hitchcock cabinet, on hard argillaceous sandstone, from Gill, Massachusetts.

Genus **Argoides** E. Hitchcock. (Cyclops-like.)

Argoides E. Hitchcock, **'45b**, p. 24.

Argozoum E. Hitchcock, **'58**, p. 81.

Generic characters. Bipedal, leptodactylous, tridactylous. Toes curved, the latter ones more or less outward and upward behind, so as to be keel shaped. Digitigrade, rarely showing a heel.

Argoides isodactyletus (E. Hitchcock).

Argoides isodactyletus E. Hitchcock, **'45b**, p. 24.

Argoides minimus E. Hitchcock, **'45b**, p. 24.

Argozoum paridigitatum E. Hitchcock, **'58**, p. 82, pl. 14, fig. 3; pl. 35, fig. 4; pl. 39, fig. 1.

Plesiornis aequalipes E. Hitchcock, **'58**, p. 104.

Specific characters. Pes: divarication of digits II and III, 40° to 50°; of III and IV, 40° to 50°; of II and IV, 80° to 100°. Length of digit II, .023 m.; of III, .033 m.; of IV, .025 m. Distance between the lateral tips, .027 m. Length of foot, .030 m.; of the step, .152 m. Width of trackway, .043 m.

The size coupled with the extreme length of limb in this form, strongly suggests the genus Grallator, but the other characters are so obscure that it is difficult to assure one's self of their identity.

Type, no. $\frac{25}{1}$, of the Hitchcock cabinet, on red shale, with shrinkage cracks, from the Lily pond at Turner's Falls, Massachusetts.

Argoides macrodactylotus (E. Hitchcock).

Platypterna macrodactylotus E. Hitchcock, **'45b**, p. 25.
Argozoum disparidigitatum E. Hitchcock, **'58**, p. 82, pl. 14, fig. 2.

Specific characters. Pes: divarication of digits II and III, 18° to 30°; of III and IV, 20° to 25°; of II and IV, 40° to 55°. Length of digit II, .076 m.; of III, .127 m.; of IV, .090 m. Length of foot, .140 m. Distance between lateral tips, .076 m. Length of step, .380 m. Width of trackway, .100 m.

Type, no. $\frac{37}{17}$, of the Hitchcock cabinet, from Weathersfield, Connecticut.

Argoides redfieldianus E. Hitchcock.

Argoides redfieldianus E. Hitchcock, **'45b**, p. 24.
Argozoum redfieldianum E. Hitchcock, **'58**, p. 81, pl. 14, fig. 1.

This track agrees in length and divarication of digits with that of *Eubrontes divaricatus* and is undoubtedly synonymous with that species. The analysis of coprolites found associated with these tracks betrays the presence of uric acid which would place the form unquestionably among the Sauropsida but not necessarily with the birds (E. Hitchcock, **'58**, p. 43).

Argoides robustus E. Hitchcock.

Argoides robustus E. Hitchcock, **'45b**, p. 24.

This form is not mentioned in any subsequent work, and should therefore be dropped from the list. What disposition was made of the specimens cannot be determined.

Genus **Tarsoplectrus** nom. nov. (Spurred tarsus.)

Plectropus E. Hitchcock, **'45b**, p. 24 (in part).
Plectropterna E. Hitchcock, **'58**, p. 108 (in part) for *Plectropus*, preoccupied.

Generic characters. Bipedal, tetradactyl, plantigrade, heel narrow, tapering backward, not always wholly impressing. Limbs long; trackway narrow. No phalangeal pads nor distinct claws.

This genus as at present restricted contains but two species, *T. angustus* (E. Hitchcock) and *T. elegans* (C. H. Hitchcock). The name Plectropterna unfortunately cannot be retained, as the type species, *P. minitans*, proves to be synonymous with *Anomoepus intermedius*, the old generic name becoming thus a synonym for Anomoepus.

The type species is *Tarsoplectrus angustus*.

Tarsoplectrus angustus (E. Hitchcock).

Plectropterna angusta E. Hitchcock, **'58**, p. 110, pl. 18, fig. 4 ; pl. 36, fig. 3.

Specific characters. Pes : divarication of digits I and II, 95° ; of II and III, 22° ; of III and IV, 25 ; of II and IV, 47°. Length of digit I, .018 m.; of II, .051 m.; of III, .071 m.; of IV, .046 m. Distance between lateral tips, .040 m. Length of foot, .110 m. Length of step, .305 m. Width of trackway, .068 m. Toes slightly curved. Hallux strongly recurved arising about the middle of the length of the heel.

Type specimen, no. $\frac{33}{39}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Tarsoplectrus elegans (C. H. Hitchcock).

Plectropterna elegans C. H. Hitchcock, **'89b**, pp. 122, 125.

Specific characters. Pes : divarication of digits II and III, 30° ; of III and IV, 40° ; of II and IV, 70°. Length of digit I, .023 m.; of II, .026 to .045 m.; of III, .051 to .076 m.; of IV, .038 to .045 m. Length of foot, .127 to .132 m. Distance between lateral tips, .050 to .060 m. Length of step, .457 to .533 m. Width of trackway, .077 m.

Type specimens, nos. 53, 91, and 242, in the Mt. Holyoke cabinet, from Weathersfield, Connecticut.

Genus **Polemarchus** E. Hitchcock. (A leader in war.)

Polemarchus E. Hitchcock, **'45b**, p. 24 ; **'58**, p. 107, pl. 18, fig. 1 ; pl. 59, fig. 3.

Generic characters. Bipedal, tetradactyl, plantigrade, with broad heel and with a large, half rotated hallux. Toes slender in the track, but the latter, which is of shale, has doubtless caved in to some extent. No pads nor claws in evidence.

Except for the presence of the hallux this form most nearly approximates Platypterna. There is but one extremely rare species: *Polemarchus gigas*.

Polemarchus gigas E. Hitchcock.

Polemarchus gigas E. Hitchcock, **'45b**, p. 24 ; **'58**, p. 107, pl. 18, fig. 1 ; pl. 59, fig. 3.

Specific characters. Pes: divarication of digits I and II, 61° ; of II and III, 20° ; of

III and IV, 25°; of II and IV, 45°. Length of digit I, .064 m.; of II, .217 m.; of III, .285 m.; of IV, .213 m.; of the heel, .097 m. Length of foot, .376 m. Width of the heel, .100 m. Distance between tips of the lateral toes, .165 to .222 m. Length of step, 1.224 m. Width of trackway, ? .350 m. The hallux is straight, the other digits curve inward.

The type specimens are nos. $\frac{26}{15}$, $\frac{26}{16}$, and $\frac{26}{17}$, of the Hitchcock cabinet, in slightly calcareous shale, the first two from the middle of the Connecticut river at Chicopee Falls, Massachusetts, the last from near Cabotville, Massachusetts.

Genus **Plesiornis** E. Hitchcock. (Near a bird.)

Plesiornis E. Hitchcock, **'58**, p. 102.

Generic characters as given by Hitchcock: "tridactylous, pachydactylous, hind foot slightly the largest. Toes slightly turned in towards the line of direction; terminated by blunt claws, or pellets. Highly ornithoid; the tracks distinguished from those of birds only by being arranged two by two along the median line, with a wide interval between." The footprints thus described by Hitchcock under this genus are doubtless in every instance those of two animals walking one after the other, a theory which Hitchcock at first held, but afterwards abandoned on the ground that such tracks occurred too frequently to be thus explained. The so called fore foot track is a typical pes impression and never that of such a manus as one would expect from the very Anomoepus-like appearance of the hind foot. That one animal followed another frequently is not unlikely, if, as the present author believes, the animals resorted to the congregating places for breeding purposes, and the slight difference in size could readily be a sexual character. The quadrupedal nature of the tracks seems amply disproved. Some of the species are referable to known bipedal forms, the others it will be necessary to retain under the present genus, whose revised characters may be thus defined: bipedal, digitigrade, tridactyl forms, digits terminated by blunt or pellet-like claws. Small forms of doubtful affinity.

Plesiornis pilulatus E. Hitchcock.

Plesiornis pilulatus E. Hitchcock, **'58**, p. 103, pl. 17, fig. 8; pl. 36, fig. 4.

Specific characters. Pes: divarication of digits II and III, 35°; of III and IV, 35°; of II and IV, 70°. Length of digit II, .033 m.; of III, .053 m.; of IV, .038 m. Length of foot, .053 m. Distance between lateral tips, .038 m. Length of step, .183 m. Width of trackway, .050 m.

The foot is quite similar to that of Grallator, except for the form of the claw and the occasional presence of a spur-like process on the inner side of the foot.

Type, no. $\frac{13}{1}$, of the Hitchcock cabinet, on gray sandstone from Turner's Falls, Massachusetts.

Plesiornis mirabilis E. Hitchcock.

Plesiornis mirabilis E. Hitchcock, **'65**, p. 35, pl. 20.

Possibly referable to *Anchisauripus tuberosus* E. Hitchcock, especially the larger track, though the smaller track does not resemble it very closely. This species is based upon a single specimen, no. $\frac{51}{16}$, of the Hitchcock cabinet, which is peculiar not only in the lack of similarity of the two sets of footprints, but also in the presence of more or less parallel markings which may be due to dragging tails or limbs or to some other body which may have been drawn along.

Plesiornis giganteus C. H. Hitchcock.

Plesiornis giganteus C. H. Hitchcock, **'89b**, pp. 118, 122, 126.

Probably referable to *Anchisauripus minusculus*.

Genus **Sillimanius** E. Hitchcock. (For B. Silliman.)

Sillimanius E. Hitchcock, **'45b**, p. 24.
Ornithopus E. Hitchcock, **'48**, p. 191.

Generic characters. Bipedal, tetradactylous, hallux rotated so as to be in line with the fourth digit. Digitigrade to semiplantigrade.

This genus is founded on Weathersfield shale specimens and the true characters are obscured. The type species is *Sillimanius tetradactylus* E. Hitchcock.

Sillimanius tetradactylus E. Hitchcock.

Sillimanius tetradactylus E. Hitchcock, **'45b**, p. 24.
Ornithopus gallinaceus E. Hitchcock, **'48**, p. 192, pl. 8, fig. 1; **'58**, p. 87, pl. 14, fig. 10; pl. 58, fig. 1.

Specific characters. Pes: divarication of digits I and II, 110°; of II and III, 35°; of III and IV, 45°; of II and IV, 80°. Length of digit I, .043 m.; of II, .043 m.; of III, .076 m.; of IV, .051 m. Length of foot impression, .097 m. Distance between lateral tips, .069 m. Length of step, .178 m. Width of trackway, .064 m. Foot semiplantigrade.

Type, no. $\frac{32}{41}$, of the Hitchcock cabinet, on red shale, from Weathersfield, Connecticut.

Sillimanius gracilior E. Hitchcock.

Sillimanius gracilior E. Hitchcock, **'45b**, p. 24.

Ornithopus gracilior E. Hitchcock, **'48**, p. 193, pl. 8, fig. 2; **'58**, p. 88, pl. 14, fig. 11; pl. 58, fig. 7.

Specific characters. Pes: divarication of digits I and II, 85°; of II and III, 35°; of III and IV, 52°. Length of digit I, .010 m. (impression); of II, .021 m.; of III, .032 m.; of IV, .023 m. Distance between lateral tips, .043 m. Length of foot impression, .043 m. Length of step, .153 m. Width of trackway, .115 m. Foot digitigrade, entire length of the hallux not impressing.

The type specimen is no. $\frac{31}{75}$, of the Hitchcock cabinet, on red shale from Weathersfield, Connecticut.

Genus **Steropoides** E. Hitchcock. (Like Steropus, a Cyclops.)

Steropoides E. Hitchcock, **'45b**, p. 24.

Steropezoum E. Hitchcock, **'48**, p. 182.

Tridentipes E. Hitchcock, **'58**, p. 88 (to replace *Steropezoum*).

Generic characters. Bipedal, tetradactyl, subdigitigrade to semiplantigrade. Tarsus sloping upward so that the impression often ends in ridges and furrows. The hallux is rotated backward so as to be in line with digit IV.

The members of this genus are very similar to those of Sillimanius especially to *S. tetradactylus* E. Hitchcock. *Steropoides elegans* may be taken as the type.

Steropoides elegans E. Hitchcock.

Steropoides elegans E. Hitchcock, **'45b**, p. 24.

Steropoides elegantior E. Hitchcock, **'45b**, p. 24.

Steropezoum elegans E. Hitchcock, **'48**, p. 183, pl. 5, fig. 2.

Steropezoum elegantius E. Hitchcock, **'48**, p. 184, pl. 5, fig. 3.

Tridentipes elegans E. Hitchcock, **'58**, p. 90, pl. 15, fig. 2; pl. 45, fig. 6; pl. 52, figs. 8, 11.

Specific characters. Pes: divarication of digits I and II, 75°; of II and III, 65°; of III and IV, 65°; of II and IV, 125°. Length of digit I, .046 m.; of II, .046 m.; of III, .071 m.; of IV, .056 m. Distance between lateral tips, .089 m. Length of heel impression, .064 m. Width of heel, .013 m. Length of foot, .135 m. Length of step, .250 to .500 m. Width of trackway, .178 m.

This species is much smaller than the better known *S. ingens*, but very similar to it in form.

Type specimen, no. $\frac{26}{21}$, of the Hitchcock cabinet, is on red shale from Turner's Falls, Massachusetts.

Steropoides ingens E. Hitchcock.

Steropoides ingens E. Hitchcock, **'45b**, p. 24.

Sillimanius adamsanus E. Hitchcock, **'45b**, p. 24.

Steropezoum ingens E. Hitchcock, **'48**, p. 182, pl. 5, fig. 1.

Ornithopus adamsanus E. Hitchcock, **'48**, p. 191, pl. 7, fig. 5.

Tridentipes ingens E. Hitchcock, **'58**, p. 89, pl. 15, fig. 1.

Specific characters. Pes: divarication of digits I and II, 80°; of II and III, 50°; of III and IV, 58°; of II and IV, 107°. Length of digit I, .127 m.; of II, .203 m.; of III, .242 m.; of IV, .145 m. Distance between lateral tips, .282 m. Length of heel impression, .230 m. Length of foot, .460 m.; of the step, 1.020 to 2.020 m.

This is a large but very peculiar track as the metatarsal bones, the so called heel, make a broad and deep impression shoaling out toward the rear as though that segment of the leg were borne at a decided slant. The digits are long and very slender or else the mud has slipped into the track as soon as the foot was withdrawn. There are no digital pad impressions or other characters preserved. The foot is more lacertilian than avian and is totally unlike the typical dinosaurian tracks. Yet from its bipedal gait and the number of digits, the maker of the impression must have been a dinosaur, though unlike any form whose skeletal remains are known.

The type specimen is no. $\frac{16}{12}$, of the Hitchcock cabinet, on gray micaceous sandstone, from Gill, Massachusetts. It is also found on the White hall, New Jersey, slab of red shale, in the Rutgers college museum.

Steropoides infelix Hay.

Steropoides infelix O. P. Hay, **:02**, p. 552 (to replace *elegantior* a name already used within the genus).

Tridentipes elegantior E. Hitchcock, **'58**, p. 90, pl. 15, fig. 3; pl. 45, fig. 1 (not *Steropezoum elegantius*, **'48**).

Specific characters. Pes: divarication of digits I and II, 108°; of II and III, 32°; of III and IV, 44°; of II and IV, 75°. Length of digit I, .010 m.; of II, .015 m.; of III, .029 m.; of IV, .023 m. Distance between lateral tips, .028 m. Length of heel impression, .018 m.; of foot, .045 m. Length of step, .135 m. Width of trackway, .045 m.

Type, no. $\frac{19}{9}$, of the Hitchcock cabinet, on reddish shale from Turner's Falls, Massachusetts.

Steropoides loripes (E. Hitchcock).

Ornithopus loripes E. Hitchcock, **'48**, p. 193, pl. 8, fig. 3.
Tridentipes insignis E. Hitchcock, **'58**, p. 91, pl. 15, fig. 4; pl. 45, fig. 3; pl. 47, fig. 2.

Specific characters. Pes: divarication of digits I and II, 55°; of II and III, 45°; of III and IV, 50°; II and III, 95°. Length of digit I, .081 m.; of II, .109 m.; of III, .135 m.; of IV, .109 m. Distance between lateral tips, .160 m. Length of heel impression varies up to .050 m. Length of foot, .152 to .178 m. Length of step, .400 to .567 m. Width of trackway, .317 m.

A long limbed, blunt clawed form; subdigitigrade.

Type specimens, nos. $\frac{1}{4}$ and $\frac{5}{11}$, of the Hitchcock cabinet, on micaceous sandstone, from near Montague, Massachusetts.

Steropoides uncus (E. Hitchcock).

Tridentipes uncus E. Hitchcock, **'58**, p. 91, pl. 15, fig. 5; pl. 46, fig. 1.

Specific characters. Pes: divarication of digits I and II, 22°; of II and III, 48°; of III and IV, 44°; of II and IV, 90°. Length of digit I, .028 m.; of II, .043 m.; of III, .056 m.; of IV, .036 m. Distance between lateral tips, .056 m. Length of heel, .028 m.; of the foot, .082 m. Length of step, .215 to 227 m. Width of trackway, .155 m.

S. uncus differs markedly from the other members of the genus in the short step and wide trackway, and also in the position of the hallux which is only semirotated.

The type is no. $\frac{6}{1}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Genus **Lagunculapes** E. Hitchcock. (Flask foot.)

Lagunculapes E. Hitchcock, **'58**, p. 132.

Generic characters. Bipedal, digitigrade, tetradactyl, with the clawless digits widely radiating and more or less flask- or club-shaped, dilating toward their tips; clawless.

There is but one species, *L. latus* E. Hitchcock.

Lagunculapes latus E. Hitchcock.

Lagunculapes latus E. Hitchcock, **'58**, p. 132, pl. 24, fig. 1; pl. 45, fig. 4.

Specific characters. Pes: divarication of digits I and II, 50°; of II and III, 70°; of

III and IV, 65°; of I and IV, 180°. Length of digit I, .013 m.; of II, .014 m.; of III, .020 m.; of IV, .015 m. Length of foot, .022 m. Width of foot, .032 m. Length of step, .076 m. Width of trackway, .076 m.

Hitchcock considers this form a batrachian because of the similarity to Proteus in number of toes and absence of claws. He also likens the form of the toes to that of the toes of the lizard, Anolis. The bipedal walk would seem to associate the form with the Reptilia though it hardly agrees with our conception of a dinosaur.

Type, no. $\frac{33}{29}$, of the Hitchcock cabinet, on gray shale from Turner's Falls, Massachusetts.

Forms occasionally quadrupedal.

Genus **Xiphopeza** E. Hitchcock. (Sword foot.)

Xiphopeza E. Hitchcock, **'48**, p. 239.

Generic characters. Quadrupedal, possibly not habitually so; plantigrade; the tetradactylous pes much larger than the manus which, in the known specimens, impresses but three digits.

Xiphopeza triplex E. Hitchcock.

Xiphopeza triplex E. Hitchcock, **'48**, p. 239, pl. 15, fig. 8; **'58**, p. 113, pl. 20, fig. 6; pl. 52, figs. 3, 4, 6.

Specific characters. Pes: divarication of digits I and II, 90°; of II and III, 40°; of III and IV, 50°. Length of digit I, .013 m.; of II, .020 m.; of III, .038 m.; of IV, .028 m.; of the heel, .030 m. Length of foot, .066 m. Distance between lateral tips, .038 m. Breadth of heel, .012 m. Length of step, .102 m. Width of trackway, .115 m.

Manus: but three digits impressing, about .010 m. in length.

Type specimen, no. $\frac{41}{26}$, of the Hitchcock cabinet, on gray shale from Turner's Falls, Massachusetts.

Genus **Tarsodactylus** E. Hitchcock. (Toed tarsus.)

Tarsodactylus E. Hitchcock, **'58**, p. 98.

Generic characters. Quadrupedal, digitigrade; manus pentadactylous, pes tetradactylous with broad digits and somewhat acuminate claws but without phalangeal pads. Tail trace present. A very rare group.

Tarsodactylus caudatus E. Hitchcock.

Tarsodactylus caudatus E. Hitchcock. **'58**. p. 99. pl. 17. fig. 4 ; pl. 36. fig. 2.

This form approximates *Anomoepus minimus* closely in size and proportions, being but little larger. It may prove identical.

Type specimen, no. $\frac{42}{5}$, of the Hitchcock cabinet, on shale from Turner's Falls, Massachusetts.

Tarsodactylus expansus C. H. Hitchcock.

Tarsodactylus expansus C. H. Hitchcock, **'66**, p. 301–302.

Specific characters. Pes: divarication of digits II and III, 25° ; of III and IV, 50° ; of II and IV, 75° to 80°. Length of digit II, .025 m.; of III, .037 m.; of IV, .028 m. Length of hallux claw, .005 m.; distance from foot, .010 m. Distance between lateral tips, .038 m. Length of foot, .043 m. Length of step, .127 to .178 m. Width of trackway, .140 m.

Manus: divarication of digits I and II, 30° ; of II and III, 20° ; of III and IV, 25° ; of IV and V, 25° to 30°; of I and V, 100°. Length of digit I, .012 m.; of II, .020 m.; of III, .019 m.; of IV, .015 m.; of V, .0095 m. Distance between lateral tips, .025 m. Caudal trace, slight.

This form differs from *T. caudatus* in the greater divarication of the toes; in its smaller size; in its irregular mode of walking as compared with *caudatus*, and the fact that it does not trail the toes as does the latter. This feature may be entirely due to the animal's gait at the time the impressions were made and hence may be of little importance as a distinction.

The type specimen is from near Greenfield, Massachusetts, and is preserved in the cabinet of Prof. C. H. Hitchcock, at Dartmouth college, Hanover, New Hampshire.

Genus **Harpedactylus** E. Hitchcock. (Sickle toed.)

Harpedactylus E. Hitchcock, **'45b**, p. 24.

Generic characters. Quadrupedal, tetradactylous, plantigrade; heel long, digits sometimes curved inward, sickle-like. This genus represents a group of mud tracks, at least two species of which seem referable to Anomoepodoid forms, while the third, *H. crassus,* is not so typical. The entire group seems to be of doubtful validity.

Harpedactylus tenuissimus E. Hitchcock.

Harpedactylus tenuissimus E. Hitchcock, **'45b**, p. 24.

Harpedactylus gracilis E. Hitchcock, **'58**, p. 112, pl. 20, fig. 4 ; pl. 52, fig. 5.

The known specimens are those of seated animals about the size and proportions of *Anomoepus minimus* E. Hitchcock, and possibly referable to that species.

The type specimen is no. $\frac{27}{18}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts. It seems further possible that *Plectropterna gracilis* E. Hitchcock, may also belong here, as well as *P. lineans* E. Hitchcock.

Harpedactylus gracilior E. Hitchcock.

Harpedactylus gracilior E. Hitchcock, **'65**, p. 12, pl. 3, fig. 2.

This form is very similar to the preceding species except that it is much smaller and the manus is unknown. It is impossible to refer it to any known Anomoepus because of its size, but its affinities are probably with that genus. *H. gracilior* is known from but two specimens, nos. $\frac{47}{52}$ and $\frac{55}{1}$, of the Hitchcock cabinet, both from Turner's Falls, Massachusetts.

Harpedactylus crassus E. Hitchcock.

Harpedactylus crassus E. Hitchcock, **'65**, p. 12, pl. 3, fig. 1.

This species is based upon a single badly worn specimen showing both manus and pes tracks. It is a characterless track of doubtful affinity. It could, however, have been formed by *Anomoepus scambus* as the size and proportions of fore and hind feet agree; but the subsequent slipping of the mud has distorted the impression very much.

The type specimen is no. $\frac{47}{53}$, of the Hitchcock cabinet, on gray shale; type locality unrecorded.

Subclass SYNAPSIDA Osborn.

Order *TESTUDINATA*.

Quadrupedal forms, generally with short stride and wide trackway indicating short legged, broad bodied creatures. Often with longitudinal traces which may have been made by dragging tail, limbs, or plastron. The reference of the following genera to this order is by no means certain, being based upon President Hitchcock's opinion.

Genus **Ancyropus** E. Hitchcock. (Anchor foot.)

Ancyropus E. Hitchcock, **'45b**, p. 24; **'58**, p. 138.

Generic characters. Quadrupedal, plantigrade. Pes tetra- or pentadactylous, hallux semirotated, the other digits turned outward very strongly. Manus tetradactylous, digits as in pes, but much slenderer in proportion to its length. No pad nor claw impressions are preserved.

In several of the specimens it seems as though the foot which made the impression had lain on its side rather than in the normal position, which may account for the peculiar form of the track.

Ancyropus heteroclitus E. Hitchcock.

Ancyropus heteroclitus E. Hitchcock, **'45b**, p. 24; **'58**, p. 139, pl. 25, fig. 3–4; pl. 53, fig. 1–2.

Ancyropus jacksonianus E. Hitchcock, **'45b**, p. 24.

Specific characters. Pes: length of foot, .051 m. Breadth across the toes, .033 m.; across the heel, .020 m. Average length of digits, about .010 m. Length of step, .063 m. Width of trackway, .165 m.

Manus: length, .051 m.; average length of digits, .007 to .008 m. Breadth of palm, .007 m.

The shortness of limbs, width of trackway, and the form of the feet are Chelonia-like, hence this form seems to be included in that order.

Type, no. $\frac{27}{7}$, of the Hitchcock cabinet, on gray shale from Weathersfield, Connecticut.

Genus **Chelonoides** E. Hitchcock. (Tortoise like.)

Chelonoides E. Hitchcock, **'58**, p. 140.

Generic characters. Quadrupedal; pes tridactylous, digitigrade, smaller than the plantigrade, pentadactyl manus. No claws nor pads. Limbs long, body wide.

Hitchcock's reference of this form to the Chelonia is based solely upon the width of the body, but the feet are not like those of tortoises nor is there any evidence of a dragging plastron or tail.

Chelonoides incedens E. Hitchcock.

Chelonoides incedens E. Hitchcock, **'58**, p. 140, pl. 31, fig. 3.

Specific characters. Pes: divarication of digits II and IV, 80°. Length of digit II, .017 m.; of III, .020 m.; of IV, .017 m. Length of foot, .026 m. Length of stride, .180 m. Width of trackway, .165 m.

Manus: divarication of digits II and V, 100°. Length of digit I, .010 m.; of II, .018 m.; of III, .023 m.; of IV, .020 m.; of V, .020 m.; of the heel, .028 m. Length of entire impression, .043 m.

The type specimen is no. $\frac{6}{1}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Genus **Amblypus** E. Hitchcock. (Blunt foot.)

Amblypus E. Hitchcock, **'58**, p. 143.

Generic characters. Impression of right hind foot only in all of the several specimens which exist. Pes plantigrade, tridactylous with the digits curving inward. No morphological characters. Manus unknown.

All of the specimens are probably the impressions of a single individual which may have been walking along the shore so that the surface under but one foot was in condition to take an impression. Hitchcock thinks the animal a Chelonian as the foot "approximates to that of some tortoises."

Amblypus dextratus E. Hitchcock.

Amblypus dextratus E. Hitchcock, **'58**, p. 143, pl. 25, fig. 7; pl. 48, fig. 5.

Specific characters. Pes: length of the foot, .025 m.; breadth, about .015 m. Digits not separated. Length of step, .100 to .115 m.

Type specimen, no. $\frac{34}{27}$, of the Hitchcock cabinet, on gray shale. from Turner's Falls, Massachusetts.

Genus **Helcura** E. Hitchcock. (Tail dragger.)

Helcura E. Hitchcock, **'48**, p. 244.

Generic characters. "Quadrupedal; tail and toes often dragging on the ground." Broad body trace.

These traces give absolutely no data concerning the form and structure of the feet. Hitchcock compares the markings to those left by living land tortoises and hence classes them provisionally with the Chelonia.

The species are: —

Helcura anguinea E. Hitchcock.

Helcura anguinea E. Hitchcock, **'58**, p. 141, pl. 36, fig. 9.

Specific characters. Length of stride of the same foot, .125 to .150 m. Width of trackway, .075 m.

Type specimen, no. $\frac{40}{8}$, of the Hitchcock cabinet, on gray shale, from Turner's Falls, Massachusetts.

Helcura littoralis E. Hitchcock.

Helcura littoralis E. Hitchcock, **'48**, p. 244, pl. 15, fig. 1; pl. 23, fig. 3.
Helcura caudata E. Hitchcock, **'58**, p. 140, pl. 37, fig. 3; pl. 40, fig. 1.

Specific characters. Length of stride, .150 m. Width of trackway, .125 m.

Type specimen, no. $\frac{26}{15}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Helcura surgens E. Hitchcock.

Helcura surgens E. Hitchcock, **'58**, p. 141, pl. 36, fig. 10.

Specific characters. Width of trackway, .125 to .150 m. No caudal trace.

This species is distinguished from the others by its greater width of body and the absence of a tail trace and of footprints.

Type specimen, no. $\frac{12}{8}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

INCERTAE SEDIS.

Forms habitually quadrupedal.

Genus **Eupalamopus** Hay.

Eupalamopus O. P. Hay, **:02**, p. 544 (name given as a substitute for *Palamopus* E. Hitchcock, **'48**, p. 217, preoccupied by E. Hitchcock in 1845).

Generic characters. ? Quadrupedal. Pes palmated, tetradactylous, all toes directed forward. Heel stout, bent outward. Manus not well known, about one third the length of the pes.

Eupalamopus dananus (E. Hitchcock).

Palamopus dananus E. Hitchcock, **'48**, p. 217, pl. 9, fig. 1–2.
Palamopus clarki E. Hitchcock, **'58**, p. 127, pl. 23, fig. 2; pl. 44, fig. 2.

Specific characters. Pes: divarication of digits I and II, 25°; of II and III, 30°; of III and IV, 15°. Length of digit I, .137 m.; of II, .165 m.; of III, .217 m.; of IV, .153 m., measured from the extremity of the heel. Distance between lateral tips, .120 m. Length of foot, .217 m. Length of step, .535 m. Width of trackway, .127 m.

Manus: length, .090 m.; breadth, .038 m. What appears to be the manus impression lies midway between successive tracks of the pes. There are no phalangeal impressions nor distinct claws in the footprints so that the true affinities of this very rare track cannot be learned. If it is really quadrupedal in its gait it is among the largest of such forms in the Connecticut valley.

The type specimen, which is unique, is no. $\frac{12}{1}$, in the Hitchcock cabinet, from Northampton, Massachusetts, associated with *Eubrontes approximatus* and with *Anchisauripus tuberosus, A. tuberatus,* and *A. exsertus.*

Genus **Palamopus** E. Hitchcock. (Palm foot.)

Palamopus E. Hitchcock, **'45b**, p. 24.

Sillimanius E. Hitchcock, **'45b**, p. 24 (in part).

Macropterna E. Hitchcock, **'58**, p. 128.

Dr. O. P. Hay (**:02**, p. 548) says: "This is not the Palamopus of 1848 and subsequently. The latter is here represented by Eupalamopus."

Generic characters. Quadrupedal; manus and pes of unequal size, the latter being from two to three times the length of the former. Feet plantigrade. Pes tetradactyl. Manus pentadactyl; no claw nor phalangeal pad impressions. Caudal trace sometimes present.

Palamopus anomalus E. Hitchcock.

Palamopus anomalus E. Hitchcock, **'45b**, p. 24.

Macropterna recta E. Hitchcock, **'48**, p. 235, pl. 15, fig. 6.

Specific characters. Pes: divarication of digits I and II, 10°; of II and III, 30° to 35°; of III and IV, 35°; of I and IV, 75° to 80°. Length of digit I, .023 m.; of II, .032 m.; of III, .041 m.; of IV, .028 m.; of the heel, .036 m.; of the foot, .077 m. Distance between lateral tips, .040 to .046 m. Breadth of heel, .010 to .015 m. Length of step, .195 m. Digits nearly straight.

Manus: divarication of digits I and II, 30°; of II and III, 35°; of III and IV, 35°; of I and IV, 100°. Length of digit I, .006 m.; of II, .010 m.; of III, .023 m.; of IV, .018 m. Digit V not impressing. Distance between lateral tips, .030 m.

This form is not mentioned by either Hitchcock after 1848. The only specimen which it is possible to identify among those mentioned in 1848, is the old no. 33, now $\frac{40}{64}$, of the Hitchcock cabinet and correctly referred in the catalogue to *Palamopus divaricans.*

Palamopus divaricans (E. Hitchcock).

Macropterna divaricans E. Hitchcock, **'48**, p. 237, pl. 15, fig. 7; **'58**, p. 129, pl. 23, fig. 7.

Specific characters. Pes: divarication of digits I and II, 20°; of II and III, 30°; of III and IV, 40°; of I and IV, 90°. Length of digit I, .013 m.; of II, .015 m.; of III, .027 m.; of IV, .015 m. Distance between lateral tips, .030 m. Length of heel, .043 m.; of foot, .069 m. Breadth of heel, .012 m. Length of step, .084 to .178 m. Width of trackway, .076 m.

Manus: with five digits radiating through about 180°. Length, .023 m.; breadth, .018 m.

Type specimen, no. $\frac{27}{3}$, of the Hitchcock cabinet, on red shale from Turner's Falls, Massachusetts.

Palamopus gracilipes (E. Hitchcock).

Macropterna gracilipes E. Hitchcock, **'58**, p. 129, pl. 13, fig. 6; pl. 34, fig. 1.

Specific characters. Pes: divarication of digits I and II, 40°; of II and III, 25°; of III and IV, 25°; of I and IV, 90°. Length of digit I, .004 m.; of II, .007 m.; of III, .008 m.; of IV, .007 m.; of heel, .007 m.; of foot, .015 m. Length of step, .060 to .070 m. Width of trackway, .030 m.

Manus: but four digits impressing; form and divarications about that of the pes. Length, .005 m.; breadth, .009 m.

Type specimen, no. $\frac{35}{23}$, of the Hitchcock cabinet, on shale from Turner's Falls, Massachusetts.

Palamopus rogersianus (E. Hitchcock).

Sillimanius rogersianus E. Hitchcock, **'45b**, p. 24.

Macropterna rhynchosauroidea E. Hitchcock, **'48**, p. 233, pl. 15, fig. 9.

Macropterna vulgaris E. Hitchcock, **'58**, p. 128, pl. 23, fig. 5; pl. 35, fig. 9; pl. 37, fig. 4; pl. 48, fig. 7; pl. 49, fig. 3; pl. 59, fig. 5.

Specific characters. Pes: divarication of digits I and II, 30°; of II and III, 20°; of III and IV, 30°; of I and IV, 80°. Length of digit I, .005 m.; of II, .009 m.; of III, .013 m.; of IV, .013 m.; of the heel, .015 m.; of the foot, .028 m. Length of step, .046 m. Width of trackway, .050 m.

Manus: five digits impressing, ranging through 180°. Length, .015 m.; breadth, .011 m.

Caudal trace sinuous, not always present.

Type specimens, nos. $\frac{36}{25}$ and $\frac{39}{79}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Genus **Exocampe** E. Hitchcock.

Exocampe E. Hitchcock, **'58**, p. 142.

Generic characters. Quadrupedal. Pes tetradactylous, digitigrade, heel occasionally impressing; the three outermost digits curved outward from the line of direction.

Manus pentadactylous, about one half the length of the pes; not always impressing. Legs moderately long, as indicated by the long step and the narrow trackway. No morphological characters exhibited by the tracks.

The type species is *Exocampe arcta.*

Exocampe arcta E. Hitchcock.

Exocampe arcta E. Hitchcock, **'58**, p. 142, pl. 25, figs. 5, 6, 10; pl. 49, fig. 5.

Specific characters. Pes: divarication of outer toes, 110°. Length of digit I, .020 m.; of II, .028 m.; of III, .033 m.; of IV, .033 m. Length of heel, .020 m.; of the foot, .048 m. Length of step, .217 m. Width of trackway, .075 m.

Manus: divarication of lateral digits, 110°. Length of digit I, .009 m.; of II, .023 m.; of III, .025 m.; of IV, .025 m.; of V, .013 m. Digits much less curved than are those of the pes. Manus position in advance of the pes and much farther from the median line.

The type is no. $\frac{35}{24}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Exocampe ornata E. Hitchcock.

Exocampe ornata E. Hitchcock, **'58**, p. 143, pl. 25, fig. 11; pl. 48, figs. 1, 6.

Specific characters. Pes: divarication of lateral digits, 100° to 130°. Length of digit I, .006 m.; of II, .007 m.; of III, .010 m.; of IV, .008 m. Length of step, .055 m. Width of trackway, .025 m.

Manus: Four digits directed forward, and one to the rear; divarication of the former, 130°. Length of manus, .013 m.

Exocampe ornata differs from *E. arcta* in its smaller size and more delicate form.

Type specimens, nos. $\frac{39}{69}$ and $\frac{41}{39}$, in the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Exocampe minima E. Hitchcock.

Exocampe minima E. Hitchcock, **'65**, p. 11, pl. 18, fig. 3.

Exocampe minima C. H. Hitchcock, in E. Hitchcock, **'65**, appendix C, p. 89.

Specific characters. Pes: divarication of lateral digits, 100 to 130°. Length of digit I, .003 m.; of II, .0065 m.; of III, .008 m.; of IV, .0045 m. Very delicate claws sometimes impress. Length of step, .028 to .050 m. Width of trackway, .038 m.

Manus: one short hind toe and four front ones, the latter with a divarication of 138°. Digits vary in length from .004 to .005 m. Nearly straight.

Type specimen, no. $\frac{55}{4}$, of the Hitchcock cabinet, from Gill, Massachusetts.

Genus **Orthodactylus** E. Hitchcock. (Straight toed.)

Orthodactylus E. Hitchcock, **'58**, p. 113.

Generic characters. Quadrupedal, digitigrade. Pes with four long, straight digits, diverging but little; clawless and without phalangeal pads. Manus pentadactyl, digits ranging through 180° or more of divarication. Impression just in advance of that of the pes.

Hitchcock classes these forms with the lizards but their true position seems extremely doubtful as the data which they furnish is so meager.

Orthodactylus floriferus E. Hitchcock.

Orthodactylus floriferus E. Hitchcock, **'58**, p. 114, pl. 20, fig. 7; pl. 45, fig. 2.

Specific characters. Pes: divarication of digits I and II, 12.5°; of II and III, 4°; of III and IV, 9.5°; of I and IV, 25°. Length of digit I, .015 m.; of II, .020 m.; of III, .030 m.; of IV, .018 m. Distance between lateral tips, .013 m. Axis of foot turned outward 35° to 40°. Length of step, about .180 m. Width of trackway, .182 m.

Manus: with subequal digits about .013 m. in length, ranging through 180°.

Type specimen, no. $\frac{6}{1}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Orthodactylus introvergens E. Hitchcock.

Orthodactylus introvergens E. Hitchcock, **'58**, p. 114, pl. 20, fig. 8; pl. 51, fig. 1.

Specific characters. Pes: divarication of lateral toes, rarely more than 20°. Digits straight, very narrow, from .020 to .032 m. in length. Length of foot, .039 m. Distance between lateral tips, .025 m. Length of step, .054 m. Width of trackway, .083 m.

Manus: digits somewhat curved, about half the length of the pes. The axis of both manus and pes turn in toward the median line, a fact which constitutes the main point of difference between this and the preceding species, in which the reverse is true.

The type specimen is no. $\frac{32}{50}$, of the Hitchcock cabinet, on red shale from Turner's Falls, Massachusetts.

Orthodactylus linearis E. Hitchcock.

Orthodactylus linearis E. Hitchcock, **'58**, p. 115, pl. 20, fig. 9; pl. 48, fig. 4.

Specific characters. Pes: digits nearly parallel, the divergence of the lateral ones being not over 20°. Digits ranging in length from .007 to .013 m. Length of step, .043 m. Width of trackway, .038 m.

Manus: apparently similar to the pes though much slenderer.

This species is much smaller and more slender than the others of its genus. The fact of its dragging tail and feet in the type specimen is probably only accidental and not a specific habit.

The type is no. $\frac{27}{15}$, of the Hitchcock cabinet, on red shale from Turner's Falls, Massachusetts.

Genus **Antipus** E. Hitchcock. (Opposite foot.)

Antipus E. Hitchcock, **'58**, p. 115.

Generic characters. Quadrupedal, digitigrade. Pes tetradactylous, manus pentadactylous, without claw or phalangeal impressions.

This genus is named from the peculiar position of the tracks on the slab, those of the manus and pes pointing in nearly opposite directions. This is probably due to the fact that the lasting impression was made in a particular stage in the creature's walk which was evidently similar to the sprawling gait of the lizards and turtles. The tracks, aside from their position, resemble most closely those of the genus Sustenodactylus.

Antipus flexiloquus E. Hitchcock.

Antipus flexiloquus E. Hitchcock, **'58**, p. 115, pl. 20, fig. 10.

Specific characters. Pes: divarication of lateral digits, 60°. Length of digit I (the outermost as the impression lies), .018 m.; of II, .020 m.; of III, .020 m.; of IV, .019 m. Length of foot, .029 m. Distance between lateral tips, .025 m. Length of step, .038 to .084 m. Width of trackway, .127 m.

Manus: divarication of lateral digits, 131°. Length of hand, .023 m.; breadth, .021 m.

The type is no. $\frac{41}{52}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Antipus bifidus E. Hitchcock.

Antipus bifidus E. Hitchcock, **'58**, p. 116, pl. 36, fig. 8; pl. 48, fig. 10.

This is an extremely doubtful species.

Genus **Sustenodactylus** nom. nov. (Running to a narrow point.)

Stenodactylus E. Hitchcock, **'58**, p. 116 (name preoccupied).

Generic characters. Quadrupedal, digitigrade; pentadactyl manus and pes. Digits extremely slender and tapering, without claws or pads. Pes about twice the size of the manus.

Sustenodactylus curvatus (E. Hitchcock).

Stenodactylus curvatus E. Hitchcock, **'58**, p. 116, pl. 20, fig. 11; pl. 34, fig. 3.

Specific characters. Pes: divarication of the lateral digits, 70°. Length of digit I, .018 m.; of II, .020 m.; of III, .026 m.; of IV, .022 m.; of V, .0065 m., vestigial. Length of foot, .026 m. Length of step, .090 m. Width of trackway, .064 m.

Manus: divarication of lateral digits, 180°. Length of digit I, .006 m.; of II, .007 m.; of III, .013 m.; of IV, .014 m.; of V, .003 m.

Type specimen, no. $\frac{34}{43}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Genus **Isocampe** E. Hitchcock. (Equal curve.)

Isocampe E. Hitchcock, **'58**, p. 119.

Generic characters. Quadrupedal; manus and pes of unequal size, the former tetradactylous, possibly pentadactylous; the latter tetradactylous. Digits of the pes nearly parallel and curved toward the median line; those of the manus nearly straight, divergent. No pads nor claws. Digitigrade; with a caudal trace. A short limbed, broad bodied form.

Isocampe strata E. Hitchcock.

Isocampe strata E. Hitchcock, **'58**, p. 120, pl. 20, fig. 5; pl. 36, fig. 5.

Specific characters. Pes: digits parallel. Length of digit I, .042 m.; of II, .051 m.; of III, .058 m.; of IV, .055 m. Length of step, .161 m. Width of trackway, .078 m.

Manus: divarication of digits I and II, 5°; of II and III, 5°; of III and IV, 25°; of I and IV, 35°. Length of digit I, .028 m.; of II, .043 m.; of III, .030 m.; of IV, .028 m. Position of manus a little in advance of, and within the pes impression.

Type specimens, no. $\frac{40}{62}$, from Turner's Falls, Massachusetts, and no. $\frac{26}{4}$, from Middletown, Connecticut, both in the Hitchcock cabinet.

Genus **Shepardia** E. Hitchcock.

Shepardia E. Hitchcock, **'58**, p. 131.

Generic characters. Quadrupedal; feet nearly equal in size. Manus pentadactylous. Pes with a vestigial fifth digit; apparently webbed.

Shepardia palmipes E. Hitchcock.

Shepardia palmipes E. Hitchcock, **'58**, p. 131, pl. 24, fig. 2.

Specific characters. Pes: divarication of digits I and II, 10°; of II and III, 13°; of III and IV, 14°; of I and IV, 37°. Length of digit I, .013 m.; of II, .025 m.; of III, .030 m.; of IV, .023 m. Distance between lateral tips, .022 m. Length of foot, .030 m.

Manus: divarication of digits I and II, 30°; of II and III, 25°; of III and IV, 20°; of IV and V, 30°. Length of digit I, .010 m.; of II, .018 m.; of III, .023 m.; of IV, .026 m.; of V, .010 m. Distance between lateral tips, .018 m.

Type specimen in the Shepard collection at Amherst college, from Turner's Falls, Massachusetts.

Genus **Comptichnus** E. Hitchcock. (Elegant track.)

Comptichnus E. Hitchcock, **'65**, p. 9.

Generic characters. Quadrupedal, tetradactylous, digitigrade. Digits of the pes broad, showing neither claw nor phalangeal impressions, those of the manus making peculiar oval marks.

Comptichnus obesus E. Hitchcock.

Comptichnus obesus E. Hitchcock, **'65**, p. 9, pl. 5, fig. 4; pl. 18, fig. 6.

Specific characters. Pes: divarication of digits I and II, 28°; of II and III, 20°; of III and IV, 14°. Length of digit I, .0065 m.; of II, .009 m.; of III, .013 m.; of IV, .010 m. Length of foot, .015 m. Length of step, .065 m. Width of trackway, .038 m.

Manus: four oval impressions, three slightly radiating in front, one behind. Length of the track, .008 m.

Type specimen, no. $\frac{55}{5}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Genus **Arachnichnus** E. Hitchcock. (Spider track.)

Arachnichnus E. Hitchcock, **'58**, p. 117.

Generic characters. Quadrupedal, plantigrade. Pes tetradactylous, as is also the impression of the manus. Limbs moderately long; body wide.

Arachnichnus dehiscens E. Hitchcock.

Arachnichnus dehiscens E. Hitchcock, **'58**, p. 117, pl. 20, fig. 12–13; pl. 38, fig. 2.

Specific characters. Pes: divarication of lateral anterior digits, 150°. Length of foot, .028 m.; breadth, .017 m. Length of step, .076 to .114 m. Width of trackway, .076 m.

Manus: divarication of lateral digits, 180°. Length of impression, .009 m. Breadth, .013 m.

The footprints are obscured by radiating sun cracks but their nearest affinity seems to be with Palamopus.

Type specimen, no. $\frac{51}{18}$, of the Hitchcock cabinet, on shale from Turner's Falls, Massachusetts (figured in E. Hitchcock, **'65**, pl. 17, fig. 2).

Genus **Triaenopus** E. Hitchcock. (Anchor foot.)

Triaenopus E. Hitchcock, **'45b**, p. 24.

Generic characters. Author's description: "Quadrupedal, tetradactylous on both fore and hind feet. Toes slender and long; three directed forward with small divarication. Fourth toe coming out near the extremity of a long heel."

This is a Weathersfield shale genus and, while very common, is extremely obscure as to its true characters. It is nearly impossible to distinguish the fore and hind feet and we may have another instance[1] in which the successive tracks of two bipedal animals appear as those of one quadruped.

Triaenopus baileyanus E. Hitchcock.

Triaenopus baileyanus E. Hitchcock, **'45b**, p. 24.

Triaenopus emmonsianus E. Hitchcock, **'45b**, p. 24.

Triaenopus leptodactylus E. Hitchcock, **'58**, p. 111, pl. 19, fig. 1–9; pl. 20, fig. 1–3; pl. 45, fig. 8; pl. 52, fig. 1.

Hitchcock here substituted the name *T. leptodactylus* for the species whose pes was formerly described as *T. baileyanus*, the manus as *T. emmonsianus*. The name *T. baileyanus* takes precedence.

Type specimen, no. $\frac{31}{27}$, of the Hitchcock cabinet, on red shale, from Weathersfield, Connecticut.

---

[1] *Vide* Plesiornis, p. 521.

Genus **Cunichnoides** E. Hitchcock. (Dog-like track.)

Cunichnoides E. Hitchcock, **'58**, p. 54.

Generic characters. Quadrupedal; fore feet rather the smaller. Ball of the foot making a distinct impression with at least four circular impressions arranged nearly on a semicircle in front of that made by the ball. No claw impressions.

This footprint bears a rather faint resemblance to that of a dog or cat, especially the latter because of the absence of claws, but the impression which would represent the ball of the foot is not differentiated from the impressions of the digits as in the modern Carnivora. The impressions are certainly not reptilian and may possibly be mammalian, but it seems likely, in view of their rarity, that the creature which made the tracks was abnormal.

Cunichnoides marsupialoideus E. Hitchcock.

Cunichnoides marsupialoideus E. Hitchcock, **'58**, p. 55, pl. 9, fig. 5; pl. 40, fig. 2.

Type specimen, no. $^{29}_{2}$, of the Hitchcock cabinet, from Portland, Connecticut.

GENERA OF DOUBTFUL VALIDITY.

Genus **Anticheiropus** E. Hitchcock. (Thumb foot.)

Anticheiropus E. Hitchcock, **'65**, p. 10.

Generic characters. Bipedal, digitigrade, tetradactyl. Digits broad but without phalangeal pads. The name is based upon the fact that one toe is offset like a thumb. In *A. pilulatus* it is evidently digit II which is thus offset, whereas in *A. hamatus* it is digit IV. The latter bears a strong resemblance to *Anomoepus crassus* except that in the latter the divarication between digits III and IV is not so great.

Each species is based upon but a single specimen which in both instances may be abnormal.

Anticheiropus pilulatus E. Hitchcock.

Anticheiropus pilulatus E. Hitchcock, **'65**, p. 10, pl. 9, fig. 3.

Specific characters. Pes: divarication of digits II and III, 75°; of III and IV, 15°; of II and IV, 90°. Length, measured to rear of impression, of digit II, .255 m.; of III, .457 m.; of IV, .315 m.; of the foot, .520 m. Distance between lateral tips, .420 m. Claws broad and rounded, pellet-like. There is an oval depression beside digit II which Hitchcock attributed to the hallux but its position is such that this seems highly improbable.

This is among the largest of the footprints and is so peculiar that one can see no similarity to any other form. More material is needed before its true nature is determined.

Type specimens, nos. $\frac{10}{4}$ and $\frac{10}{5}$, counterparts, in the Hitchcock cabinet, from Montague, Massachusetts.

Anticheiropus hamatus E. Hitchcock.

Anticheiropus hamatus E. Hitchcock, **'65**, p. 10, pl. 9, fig. 1–2.

Specific characters. Pes: divarication of digits II and III, 20° to 40°; of III and IV, 90°; of II and IV, 100°. Length of digit II, .085 m.; of III, .110 m.; of IV, .050 to .060 m.; of the foot, .180 m. Distance between lateral tips, .200 m. Length of step, .400 m. There are no distinct claws though the ends of the digits are pointed.

This is certainly a questionable species.

Type specimen, no. $\frac{51}{17}$, of the Hitchcock cabinet, on red shale from Turner's Falls, Massachusetts.

Genus **Hoplichnus** E. Hitchcock. (Hoof track.)

Hoplichnus E. Hitchcock, **'48**, p. 230.

Generic characters. Quadrupedal; hind foot somewhat the largest; track hoof-shaped. These tracks have no sign of digit or claw and are doubtfully referable to vertebrates at all.

Hoplichnus equus E. Hitchcock.

Hoplichnus equus E. Hitchcock, **'58**, p. 134, pl. 24, figs. 3, 5.

Hoplichnus quadrupedans E. Hitchcock.

Hoplichnus quadrupedans E. Hitchcock, **'48**, p. 230, pl. 16, fig. 7–8; pl. 22, fig. 3.
Hoplichnus poledrus E. Hitchcock, **'58**, p. 136, pl. 24, fig. 6–7; pl. 48, fig. 9.

Both forms are from Massachusetts and the types are in the Hitchcock ichnological cabinet, nos. $\frac{29}{3}$ and $\frac{36}{1}$, respectively.

Genus **Toxichnus** E. Hitchcock. (Bow track.)

Toxichnus E. Hitchcock, **'65**, p. 12.

Generic characters. Quadrupedal, digitigrade, tetradactylous, leptodactylous.

This genus with its single species, *T. inaequalis*, is known from but two specimens which are somewhat dissimilar and whose true characters cannot be learned. Hence it is very doubtful whether this should be considered a valid genus.

Toxichnus inaequalis E. Hitchcock.

Toxichnus inaequalis E. Hitchcock, **'65**, p. 12, pl. 5, fig. 5.

Genus **Trihamus** E. Hitchcock. (Three hooks.)

Trihamus E. Hitchcock, **'65**, p. 9.

Generic characters. Bipedal, tridactyl, digitigrade; heel large, toes slender, inwardly curving like hooks.

This genus was founded upon a single specimen of two successive tracks.

Trihamus elegans E. Hitchcock.

Trihamus elegans E. Hitchcock, **'65**, p. 9, pl. 2, fig. 3.

Specific characters. Pes: divarication of digits II and IV, 70° to 80°. Length of digit II, .015 m.; of III, .019 m.; of IV, .023 m. Length of heel, .008 m.; of the foot, .030 m. Distance between lateral tips, .020 to .023 m. Length of step, .140 m.

This form is long of limb and seems to have had proportions which suggest a small Grallator, but the foot characters so far as can be learned are quite different.

The type is no. $\frac{47}{30}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Trihamus magnus C. H. Hitchcock.

Trihamus magnus C. H. Hitchcock, **'89b**, pp. 118, 126.

Hitchcock describes this form as being very like *T. elegans*, save in size. Length of step, .150 m.

Type, in Mt. Holyoke museum.

Genus **Typopus** E. Hitchcock. (Type, Syriac, foot.)

Typopus E. Hitchcock, **'45b**, p. 25.

This genus seems to be founded upon abnormal feet, distorted beyond recognition, and while two specimens exist of each species the tracks were found in each case well within one animal's range.

Typopus abnormis E. Hitchcock.

Typopus abnormis E. Hitchcock, **'45b**, p. 25; **'58**, p. 105, pl. 17, fig. 9; pl. 45, fig. 7.

This form is much larger than the following species.

Type specimens, nos. $\frac{19}{1}$ and $\frac{19}{2}$, of the Hitchcock cabinet, from Turner's Falls, Massachusetts.

Typopus gracilis E. Hitchcock.

Typopus gracilis E. Hitchcock, **'58**, p. 106, pl. 17, fig. 10.

Founded upon a single track and its counterpart on the red shale of Weathersfield, Connecticut; nos. $\frac{31}{34}$ and $\frac{31}{46}$ of the Hitchcock cabinet.

CONCLUSIONS.

The creatures, the record of whose existence has remained impressed upon the ancient shales and sandstones, may be divided into two groups in accordance with their mode of progression: those of bipedal and those of quadrupedal gait. The former, it may be safely assumed, are, in all probability, dinosaurs, for aside from man, many birds, and some modern lizards, they are the only vertebrates whose gait when erect could have been a true walk or run with alternating steps, which without exception, the bipedal tracks show, there being no instance of the record of a jumping form. The presence of birds in the new red sandstone has not been proven, lizards are never *habitual* bipeds, man is clearly out of the question, hence by elimination we narrow the possible origin of such tracks down to the dinosaurian forms. This conclusion is strengthened by the presence of the fossil bones of the *Anchisauridae*, a family of primitive carnivorous dinosaurs having affinities with the Megalosauria.

The most abundant of the tracks are attributable to members of that family, creatures ranging in size from about seven to fourteen feet, so truly bipedal that the manus and tail never impress. The pes is tetradactyl but only exceptionally does the claw of the strong grasping hallux leave a mark. The claws are rather pointed and the whole foot is very bird-like. These footprints form a natural group to which the generic name of Anchisauripus is given and which corresponds to the family *Anchisauridae*.

Allied to Anchisauripus is another carnivorous form whose foot is more specialized than that of the former in the enfeeblement of the hallux and increase of weight which has rendered the foot flatter and its pads more complex. This creature, Gigandipus, reminds one strongly of the Jurassic Allosaurus though in the latter the claws were probably more trenchant and the whole foot more efficient as a grasping organ. Gigandipus, known from but one specimen, shows a sinuous caudal trace. The dragging of the tail probably was not habitual, but occurred only when the animal was slowing down before stopping.

Another abundant genus is Grallator characterized by very long limbs and small, compact feet without an impressing hallux and with no tail trace. The proportions of length of limbs to those of feet are the same as in the bustards and the forms which made the tracks were probably aberrant carnivores of habits somewhat similar to those of wading birds, possibly feeding upon feebler reptiles and amphibians, or on fish. In considering the probable relationship of this genus to genera known from their skeletal remains one is reminded strongly of Ornithomimus, a Cretaceous Compsognathoid dinosaur. Grallator comprises for the most part, small forms, the smallest species, *G. gracilis*, indicating a creature but two thirds the size of Compsognathus, the smallest known dinosaur, whose dimensions may be compared with those of the domestic cat.

Among the habitually bipedal forms, those which never impress the manus, is one group to which the name Eubrontes has been given. It includes larger and heavier forms than Anchisauripus with more blunted claws, but Hitchcock included it with the latter under the name Eubrontes and the later name Brontozoum. The two genera are so different in character that the present author is constrained not only to separate them generically but ordinally as well, for the lack of a grasping hallux, the heavy, slow moving tread, and the blunter claws are surely not carnivorous characteristics, but seem to point rather to an herbivorous habit of life. It may be that instead of being Orthopod or Predentate dinosaurs the Eubrontes represent another group of aberrant Carnivora, which like the condor (*Sarcorhamphus gryphus*) because of carrion feeding habits, did not retain the raptorial claws of its predacious allies. The genus Eubrontes while few as to species contains some of the most impressive forms which are fairly numerous as to individuals. *Eubrontes giganteus* represents an animal of massive proportions and of about twenty feet in length, which is nearly the maximum for American Triassic dinosaurs, though much inferior in size to those of the Jurassic and Cretaceous periods. Dinosaurs beyond question herbivorous in their habits and hence belonging to the order Orthopoda, are the occasionally quadrupedal forms which, though walking on the hind feet, placed the fore feet on the ground while sitting. This shows that on both manus and pes the claws are short and rounded and no longer subserve a grasping function. The particular interest which attaches to this fact is that it is the first evidence we have of Orthopoda or Predentate dinosaurs in the Trias, for their skeletal remains are entirely unknown either in this country or in Europe from the rocks of that period.

Anomoepus, the most characteristic genus among the herbivorous forms, had a pentadactyl manus with rounded claws and a tetradactyl pes with somewhat longer, but still blunted claws. The hallux was but half rotated and therefore ill fitted for grasping and there was a long metatarsus, or heel, on which the creature rested. The tail sometimes dragged just before the owner came to rest but at other times was held clear of the ground as a counterpoise to the anterior part of the body as in other genera. Anomoepus represents a group of small, lightly built creatures ranging in size from *A. minimus*, about three feet in length, to *A. crassus*, a New Jersey form, six feet long. They are among the most numerous and interesting of all of the ichnite genera with the exception of Anchisauripus.

The genus Fulicopus, which the writer has separated from the preceding group, shows a greater amount of weight borne on the hind limbs while sitting, the manus resting but lightly as with the kangaroo. The feet resemble those of Anchisauripus more than those of Anomoepus, there being less divarication or diverging of the digits, though the position of the hallux is as in the latter genus. A curious heart shaped impression frequently occurs just behind and between the impressions of the heels and this was attributed by Hitchcock to the end of a truncated tail, but the writer believes it to have been made by a callosity beneath the apposed extremities of the ischial bones. Hypsilophodon, of the Wealden of Europe, most nearly suggests the probable skeletal characters of the Anomoepodoid forms and as Professor Osborn has shown, presents the most primitive characters of any known Orthopod. It is difficult to conjecture the probable habits of Anomoepus, other than that the animals were herbivorous. They probably came to the mud flats mainly for breeding purposes as their tracks very frequently exhibit a distinct sexual dimorphism between the footprints of the two individuals.

A very striking though rare form, Otozoum, has been placed by the present writer among the Orthopoda although the structure of its foot is unlike that of any known dinosaur. Otozoum is probably bipedal though there is a possibility that the great pes may have obliterated the track of the much smaller manus. The foot is plantigrade, tetradactyl, with all of the digits pointing forward and with rounded pellet-like claws and a broadly expanding web or fleshy pad extending some distance beyond the ends of the digits. Its probable function was that of supporting the creature on soft mud rather than a natatorial one. The phalangeal formula of the pes is typically dinosaurian, while that of the manus, 2. 3. 3. 3. 3, is amphibian or cotylosaurian and would be absolutely unique in a dinosaur. The manus is rarely seen and is so obscure that there is a reasonable doubt as to the correctness of its interpretation. In one instance a dragging tail is shown which is absent in all other specimens and which is evidence in favor of the belief that the animal is a biped. Otozoum has the largest track of all, measuring twenty inches in length, but the author has no conception of the appearance of the creature itself.

Among the so called leptodactylous or narrow toed tracks, are many made by bipedal forms which were doubtless dinosaurs, some carnivorous, and some, judging from the manus which is occasionally seen, herbivorous in habits. The subsequent slipping of the mud after the withdrawal of the foot has obliterated most of the morphological characters from the impressions. Some of the leptodactylous forms have been identified with the better known genera and species, others which cannot be so identified because of their obscurity may nevertheless be identical with known forms, while still others evidently do not occur elsewhere. It is a notable fact that while the number of genera and species which have been erected upon these impressions is large, the number of individuals represented is proportionately small and these are mainly from one or two localities.

Of the truly quadrupedal forms the most interesting is Batrachopus, whose long limbs, tetradactyl, plantigrade pes with acuminate claws, and phalangeal formula of 2. 3. 4. 5, and whose pentadactyl manus are such as one would expect to find in the dinosaurian ancestor. It seems possible therefore, that Batrachopus represents a persistent type whose affinities are near the dinosaur stem form and which should be classed with Kadaliosaurus in the superorder Diaptosauria of Osborn. Batrachopus may have been a true dinosaur which had retained, among other primitive characters, the ancestral quadrupedal gait. The mode of progression was a true walk like that of a mammal and not the sprawling crawl of modern reptiles. Batrachopus included small forms of carnivorous habits.

There remain other quadrupedal forms, generally of small size, whose tracks, aside from the number of digits, size of the foot, and the length of limb, afford almost no data whereon to base a theory as to their affinities. Professor Osborn has likened ichnological interpretation to the deciphering of ancient cuneiform inscriptions which are utterly unintelligible unless one possesses the key. That the key to the deciphering of the dinosauroid tracks has been found seems evident, but in the attempt at the interpretation of the obscurer quadrupedal footprints the student is still very much in the dark.

AMHERST, MASS.

Bibliography.[1]

Adams, C. B.

’46. Notice of a small ornithichnite. Amer. journ. of sci. and arts, ser. 2, vol. 2, p. 215–216, text fig. 1–2

Baur, G.

’87. On the phylogenetic arrangement of the Sauropsida. Journ. of morphology, vol. 1, p. 93–104

Beasley, H. C.

’96. An attempt to classify the footprints in the new red sandstone of this [Liverpool] district. Proc. Liverpool geol. soc., 37th session, vol. 7, pt. 4, p. 391–409, pl. 1–3.

Beckles, S. H.

’51. On supposed casts of footprints in the Wealden. Quart. journ. geol. soc. London, vol. 7, p. 117

’54. On the ornithoidichnites of the Wealden. Quart. journ. geol. soc. London, vol. 10, p. 456–464, 1 text fig.

’59. On fossil footprints in the sandstone at Cummingstone. Quart. journ. geol. soc. London, vol. 15, p. 461.

’62. On some natural casts of reptilian footprints in the Wealden beds of the Isle of Wight and of Swanage. Quart. journ. geol. soc. London, vol. 18, p. 443–447, text fig. 1–4.

Bernhardi, Reinhard.

’34. [On tracks found near Hildburghausen.] Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1834, p. 641–642.

Bouvé, T. T.

’59. [On priority of discovering footprints in the Connecticut valley.] Proc. Boston soc. nat. hist., vol. 7, p. 49–53.

Brodie, P. B.

’60. On the occurrence of footsteps of Chirotherium in the upper Keuper of Warwickshire. Ann. and mag. nat. hist., ser. 3, vol. 5, p. 4.

Buckland, W.

’28. Note sur des traces de tortues observées dans le grès rouge. Ann. des sci. nat., vol. 13, p. 85–86.

’36. The Bridgewater treatises on the power, wisdom, and goodness of God as manifested in the creation. Treatise 6. Geology and mineralogy considered with reference to natural theology. London: 2 vols., 8vo.
("Fossil footsteps," vol. 1, p. 199–201.)

’39. An account of the footsteps of the Cheirotherium and five or six smaller animals in the stone quarries of Storeton hill, near Liverpool. Notices and abstracts of communications to British assoc. adv. sci., Newcastle meeting, 1838, vol. 7, p. 85.

’58. The Bridgewater treatises on the power, wisdom, and goodness of God, as manifested in the creation. Treatise 6. Geology and mineralogy considered with reference to natural theology. 3d ed., London: 2 vols., 8vo., illus.

Cook, G. H.

’85. [List of species found at Whitehall, New Jersey.] Geol. surv. of New Jersey, ann. rept. state geologist for 1885, p. 96.

Cope, E. D.

’67. [Account of extinct reptiles which approach birds.] Proc. acad. nat. sci. Philadelphia, 1867, p. 234–235.

Cotta, B.

’39a. Notitz über thierfährten im bunten sandstein bei Pölzig zwischen Ronneburg und Weissenfels. Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1839, p. 10–15.

’39b. Ueber thierfährten im bunten sandsteine bei Pölzig im Altenburgischen. Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1839, p. 617.

Croiset, —.

’35–’36. [On the footprints of Hessburg.] Bull. soc. géol. de France, vol. 7, p. 259–260.

Cunningham, J.

’38a. [On the footprints of Liverpool.] London and Edinburgh philos. mag., vol. 14, p. 148.

---

[1] Including nearly all of the literature upon Triassic and Jurassic footprints.

'38b. [An account of the footsteps of the Chirotherium.] Proc. geol. soc. London, vol. 3, p. 12–14.

'46. On some footmarks [of birds] and other impressions observed in the new red sandstone quarries of Storton, near Liverpool. Quart. journ. geol. soc. London, vol. 2, p. 410.

Cushman, J. A.

'04. A new footprint from the Connecticut valley. Amer. geologist, vol. 33, p. 154–156, pl. 6.
(*Otouphepus magnificus.*)

Dana, J. D.

'95. Manual of geology. 4th ed., New York: 8vo; 1088 pp., illus.
(See p. 752–753.)

Daubrée, A.

'57. Découverte de traces de pattes de quadrupèdes dans le grès bigarré de Saint-Valbert, près Luxeuil (Haute-Saône). Comptes rendus hebdomadaires des séances de l'acad. des sci., Paris, vol. 45, p. 646–648.

'58. Note sur la découverte de traces de pattes de quadrupèdes dans le grès bigarré de Saint-Valbert, près Luxeuil (Haute-Saône). Bull. soc. géol. de France, ser. 2, vol. 15, p. 218–221.

Deane, James.

'44a. On the fossil footmarks of Turner's Falls, Massachusetts. Amer. journ. sci. and arts, vol. 46, p. 73–77, pl. 1–2. Abstract of, in Quart. journ. geol. soc. London, vol. 1, 1845, p. 141–142.

'44b. On the discovery of fossil footmarks. Amer. journ. sci. and arts, vol. 47, p. 381–390.

'44c. Answer to the "Rejoinder" of Prof. Hitchcock. Amer. journ. sci. and arts, vol. 47, p. 399–401.

'45a. Description of fossil footprints in the new red sandstone of the Connecticut valley. Amer. journ. sci. and arts vol. 48, p. 158–167, pl. 3.

'45b. Illustrations of fossil footmarks. Boston journ. nat. hist., vol. 5, p. 277–284, text fig. 1–3.

'45c. Notice of a new species of batrachian footmarks. Amer. journ. sci. and arts, vol. 49, p. 79–81, text fig. A–B.

'45d. Fossil footmarks and rain-drops. Amer. journ. sci. and arts, vol. 49, p. 213–215, one page of figs.

'47a. Notice of new fossil footprints. Amer. journ. sci. and arts, ser. 2, vol. 3, p. 74–79, text fig. 1–4.

'47b. Fossil footprints. Amer. journ. sci. and arts, ser. 2, vol. 4, p. 448–449.

'48. Fossil footprints of a new species of quadruped. Amer. journ. sci. and arts, ser. 2, vol. 5, p. 40–41, 1 text fig.

'47–'50. Fossil footprints of Connecticut river. Journ. acad. nat. sci. Philadelphia, ser. 2, vol. 2, p. 71–74, pl. 8–9.

'56. On the sandstone fossils of Connecticut river. Journ. acad. nat. sci. Philadelphia, ser. 2, vol. 3, p. 173–178, pl. 18–20.

'61. Ichnographs from the sandstone of Connecticut river. Boston: 4to, 61 pp., 46 pls.

Degenhardt, —.

'40. [Footprints of birds from Oiva, province of Socorro, Mexico.] Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1840, p. 485.

Dollo, L.

'83. Troisième note sur les dinosauriens de Bernissart. Bull. mus. roy. d'hist. nat. de Belgique, vol. 2, p. 85–126, pl. 3–5.

Duncan, H.

'31. An account of the tracks and footmarks of animals found impressed on sandstone in the quarry of Corncockle Muir, in Dumfriesshire. Trans. roy. soc. Edinburgh, vol. 11, pt. 1, p. 194–209, pl. [8].

Edwards, A. M.

'95. Ornithichnites and jaw bone from the Newark sandstone of New Jersey. Amer. journ. sci., ser. 3, vol. 50, p. 346.

Egerton, P. G.

'38. [On the footprints of Liverpool.] London and Edinburgh philos. mag., vol. 14, p. 150.

Emerson, B. K.

'98. Geology of Old Hampshire county, Massachusetts, comprising Franklin, Hampshire, and Hampden counties. Monog. U. S. geol. surv., vol. 29, xxi + 790 pp., 35 pls.
(Ichnology, p. 400–404.)

Englehardt, —.

'37. Ueber die formation, in welcher die tatzen-abdrücke vorweltlicher thiere in der nähe von Hildburghausen auftreten, und über das vorkommen dieser abdrücke. Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1837, p. 379–388.

Eyerman, J.

'86. Footprints of the Triassic sandstone (Jura-Trias) of New Jersey. Amer. journ. sci., ser. 3, vol. 31, p. 72.

'89. Notes on geology and mineralogy. Proc. acad. nat. sci. Philadelphia, 1889, p. 32–35.

Field, R.

'60a. Ornithichnites, or tracks resembling those of birds. Amer. journ. sci. and arts, ser. 2, vol. 29, p. 361–363.

'60b. Ornithichnites. Proc. Amer. assoc. adv. sci., 13th meeting, Springfield, p. 337–340.

'60c. [The footmarks of the Connecticut river sandstones.] Proc. Boston soc. nat. hist., vol. 7, p. 316–317.

Gaudry, A.

'90. Les enchaînements du monde animal dans les temps géologiques. Fossiles secondaires. Paris. 8vo, figs. (On Chirotherium.)

Geinitz, H. B.

'63. Ueber thierfährten und crustaceen-reste in der untern Dyas. Neues jahrb. f. mineral., geol. u. palaeonto., 1863, p. 118.
(See Oppel, 1862.)

Gervais, Paul.

'57a. Sur des empreintes de pas laissées par plusiers espèces d'animaux dans le terrain Triassique des environs de Lodève. Comptes rendus hebdomadaires des séances de l'acad. des sci., Paris, vol. 45, p. 763–765.

'57b. [On *Chirotherium barthi* and tridactyl tracks of Lodève.] L'Institute, vol. 25.

Giebel, C. G.

'47–'56. Fauna der vorwelt mit steter berücksichtigung der lebenden thiere. Leipzig. 5 vols.
(See vol. 1, pt. 2, p. 34.)

Grabbe, H.

'81. Neue funde von saurier-fährten im Wealdensandsteine des Bückeberges. Verhandl. d. naturhist. verein d. preuss. Rheinlande und Westfalens, vol. 38, p. 161–164.

Haidinger, W.

'41. Ueber eine neue art von vorweltlichen thierfährten. Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1841, p. 546–548, pl. 10.

Harkness, R.

'50a. On the position of the impressions of footsteps in the Bunter sandstone of Dumfries-shire. Ann. and mag. nat. hist., ser. 2, vol. 6, p. 203–208.

'50b. Notice of a tridactylous footmark from the Bunter sandstone of Weston Point, Cheshire. Ann. and mag. nat. hist., ser. 2, vol. 6, p. 441–442.

'51. Notice of some new footsteps in the Bunter sandstone of Dumfries-shire. Ann. and mag. nat. hist., ser. 2, vol. 8, p. 90–95.

Hawkshaw, —.

'43. New red sandstone of Lymm in Cheshire. L'Institute, vol. 11.

Hay, O. P.

:02. Bibliography and catalogue of the fossil Vertebrata of North America. Bull. U. S. geol. surv., no. 179, p. 1–868.
(See p. 538–553.)

Hitchcock, C. H.

'55. Impressions (chiefly tracks) on alluvial clay, in Hadley, Mass. Amer. journ. sci. and arts, ser. 2, vol. 19, p. 391–396.

'65. [Editorial notes and some new descriptions.] In Edward Hitchcock's Supplement to the ichnology of New England (see E. Hitchcock, **'65**).

'66. Description of a new reptilian bird from the Trias of Massachusetts. Ann. lyceum nat. hist. New York, vol. 8, p. 301–302.

'71. [Account and complete list of the Ichnozoa of the Connecticut valley.] Walling and Gray's official topographical atlas of Massachusetts, p. xx–xxi.

'73. Footprints in the rocks. Pop. sci. monthly, vol. 3, p. 428–441, text fig. 1–7.

'89a. [Remarks on A. Wanner's paper on the discovery of fossil tracks in the Triassic of York county, Pa.] Proc. Amer. assoc. adv. sci., 37th meeting, Cleveland, 1888, p. 186.

'89b. Recent progress in ichnology. Proc. Boston soc. nat. hist., vol. 24, p. 117–127.

Hitchcock, Edward.

'36. Ornithichnology.—Description of the footmarks of birds, (Ornithichnites) on new red sandstone in Massachusetts. Amer. journ. sci. and arts, vol. 29, p. 307–340, pl. [1] fig. 1–20, 23–24; pl. [2], fig. 21–22, pl. [3].

'37a. Ornithichnites in Connecticut. Amer. journ. sci. and arts, vol. 31, p. 174–175.

'37b. Fossil footsteps in sandstone and graywacke. Amer. journ. sci. and arts, vol. 32, p. 174–176.

'41. Final report on the geology of Massachusetts. Northampton: 4to; 11 + 831 pp., illus.
(See p. 458–525, pl. 29–51.)

'43. Description of five new species of fossil footmarks, from the red sandstone of the valley of Connecticut river. Reports of the first, second and third meetings of assoc. of Amer. geologists and naturalists, p. 254–264, pl. 11.

'44a. Report on ichnolithology, or fossil footmarks, with a description of several new species, and the coprolites of birds, from the valley of the Connecticut river, and a supposed footmark from the valley of Hudson river, Amer. journ. sci. and arts, vol. 47, p. 292-322, pl. 3–4.
(Abstract in Neues jahrb. f. mineral., etc., 1845, p. 753–757.)

'44b. Rejoinder to the preceding article of Dr. Deane. Amer. journ. sci. and arts, vol. 47, p. 390–399.
(Reply to J. Deane, '**44b**.)

'45a. Extract of a letter from Prof. E. Hitchcock, embracing miscellaneous remarks upon fossil footmarks, the lincolnite, &c. Amer. journ. sci. and arts, vol. 48. p. 61–65.

'45b. An attempt to name, classify, and describe, the animals that made the fossil footmarks of New England. [Abstract.] Proc. 6th annual meeting assoc. Amer. geologists and naturalists, New Haven, Conn., April, 1845, p. 23–25.

'47. Description of two new species of fossil footmarks found in Massachusetts and Connecticut, or, of the animals that made them. Amer. journ. sci. and arts, ser. 2, vol. 4, p. 46–57, text fig. 1–3.

'48. An attempt to discriminate and describe the animals that made the fossil footmarks of the United States, and especially of New England. Mem. Amer. acad. arts and sci., new ser., vol. 3, p. 129–256, table, pl. 1–24.

'55. Shark remains from the coal formation of Illinois, and bones and tracks from the Connecticut river sandstone Amer. journ. sci. and arts, ser. 2, vol. 20, p. 416–417.

'56. Description of a new and remarkable species of fossil footmark, from the sandstone of Turner's Falls, in the Connecticut valley. Amer. journ. sci. and arts, ser. 2, vol. 21, p. 97–100, 1 text fig.

'58. Ichnology of New England. A report on the sandstone of the Connecticut valley, especially its fossil footmarks, made to the government of the Commonwealth of Massachusetts. Boston: 4to; xii + 220 pp., 60 pls.

'61. Remarks upon certain points in ichnology. Proc. Amer. assoc. adv. sci., 14th meeting, Newport, 1860, p. 144–156, text fig. 1–4.

'63. New facts and conclusions respecting the fossil footmarks of the Connecticut valley. Amer. journ. sci. and arts, ser. 2, vol. 36, p. 46–57, text fig. 1–2.

'65. Supplement to the Ichnology of New England. Boston: 4to; x + 96 pp., 20 pls.

'66. Supplement to the Ichnology of New England. Proc. Amer. acad. arts and sci., vol. 6, p. 85–92.

Hornstein, F.

'76. [On *Chirotherium geinitzi* of Karlshafen.] Neues jahrb. f. mineral., geol., u. palaeontol., 1876, p. 923–924.

von Humboldt, A.

'35. Note sur des empreintes de pieds d'un quadrupède dans la formation de grès bigarré de Hildburghausen en Allemagne. Ann. des sci. nat., zool., ser. 2, vol. 4, p. 135–138, pl. 5.

Huxley, T. H.

'59. On the *Stagonolepis robertsoni* (Agassiz) of the Elgin sandstones; and on the recently discovered footmarks in the sandstones of Cummingstone. Quart. journ. geol. soc. London, vol. 15, p. 440–460, pl 14.

Jardine, W.

'50. Note to Mr. Harkness's paper on "The position of the impressions of footsteps in the Bunter sandstone of Dumfries-shire." Ann. and mag. nat. hist., ser. 2, vol. 6, p. 208-209. (See R. Harkness, **'50a**.)

'53. The ichnology of Annandale or illustrations of footmarks impressed on the new red sandstone of Corncockle Muir. Edinburgh.

Jeffs, O. W.

'94. On a series of saurian footprints from the Cheshire Trias (with a note on Cheirotherium). Geol. mag., London, ser. 4, vol. 1, p. 451-454.

Kaup, J. J.

'35. [On the footprints of Hessburg.] Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1835, p. 327-328.

'35-'37. Das thierreich in seinem hauptformen systematisch beschrieben. 3 vols. Darmstadt. (See vol. 1, p. 246.)

Kent, W. Saville.

'97. The naturalist in Australia. London. xvi + 302 pp., 50 pls.

Kölonische zeitung.

'35. [On the footprints of Hessburg.] Verhandl. der mineralogische-geognostischen section während der versammlung deutscher naturforscher und ärtze in Bonn. Kolonische zeitung, 1835, no. 276.

Laspe, —.

'39. Ueber eine neue thierfährte im bunten sandsteine bei Gera. Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1839, p. 416-417, pl. 8A.

von Leonard, K. C.

'28. Schildkröten-spuren in rothen Floz-sandstein. Zeitschr. f. mineral., vol. 1.

Lesley, J. P.

'89-'90. A dictionary of the fossils of Pennsylvania and neighboring states named in the reports and catalogues of the survey. Geol. surv. Pennsylvania, rept. P 4, 1889. 3 vols., illus.

Link, —.

'35. Note sur des traces de pattes d'animaux inconnus contre-épreuvées dans le grès, près de Hildburghausen. Ann. des sci. nat., zool., ser. 2, vol. 4, p. 139-141.

Lortet, L.

'92. Les reptiles fossiles du bassin du Rhone. Archiv. mus. de l'hist. nat. Lyons, vol. 5, p. 1-139, pl. 1-12. (On Chirotherium, p. 125, pl. 12.)

Lucas, F. A.

'01. Animals of the past. New York, illus. (See p. 33-47, with 1 plate.)

Lyell, C.

'66. Elements of geology. 6th ed. New York. xvi + 803 pp., illus. (See p. 398.)

Mantell, G. A.

'46. Description of footmarks and other imprints on a slab of new red sandstone, from Turner's Falls, Massachusetts, U. S., collected by Dr. James Deane of Greenfield, U. S. Quart. journ. geol. soc. London, vol. 2, p. 38.

Marsh, Dexter.

'48. Fossil footprints. Amer. journ. sci. and arts, ser. 2, vol. 6, p. 272-274, 1 text fig.

Marsh, O. C.

'89. Notice of some new American Dinosauria. Amer. journ. sci., ser. 3, vol. 37, p. 331-336, text fig. 1-5. (*Ammosaurus* (*Anchisaurus*) *major*.)

'91. Notice of new vertebrate fossils. Amer. journ. sci., ser. 3, vol. 42, p. 265-269. (Ammosaurus and Anchisaurus, p. 267.)

'92. Notes on Triassic Dinosauria. Amer. journ. sci., ser. 3, vol. 43, p. 543-546, pl. 15-17.

'93. Restoration of Anchisaurus. Amer. journ. sci., ser. 3, vol. 45, p. 169-170, pl. 6.

'95. On the affinities and classification of the dinosaurian reptiles. Amer. journ. sci., ser. 3, vol. 50, p. 483-498, text fig. 1-11, pl. 10.

'96. The dinosaurs of North America. 16th ann. rept. U. S. geol. surv., 1894-'95, pt. 1, p. 133-414, text fig. 1-66, pl. 2-85.

(On the footprints: p. 146-147, fig. 2, and p. 151, pl. 5. On the Anchisauridae: p. 147-151, pl. 2-4.)

'99. Footprints of Jurassic dinosaurs. Amer. journ. sci., ser. 4, vol. 7, p. 227-232, text fig. 1-3, pl. 5.

Milne-Edwards, A.

'63. Mémoire sur la distribution géologique des oiseaux fossiles et description de quelques espèces nouvelles. Ann. des sci. nat., zool., ser. 4, vol. 20, p. 133-176, pl. 4.

Mitchell, J. A.

'95. The discovery of fossil tracks in the Newark system (Jura-Trias) of Frederick county, Maryland. Johns Hopkins univ. circulars, vol. 15, no. 121, p. 15-16.

Mudge, B. F.

'66. Discovery of fossil footmarks in the Liassic (?) formation in Kansas. Amer. journ. sci. and arts, ser. 2, vol. 41. (No names are given. C. H. Hitchcock regards them as artifacts).

'74. Recent discoveries of fossil footprints in Kansas.' Reprint of above, Trans. Kansas acad. sci., 1873, p. 7-9.

Murchison, R. I., & Strickland, H. E.

'40. On the upper formations of the new red sandstone system in Gloucestershire, Worcestershire, and Warwickshire; showing that the red or saliterous marls, including a peculiar zone of sandstone, represent the "Keuper" or "marnes irisées"; with some account of the underlying sandstone of Ombersley, Bromsgrove, and Warwick, providing that it is the "bunter sandstein" or "grès bigarré" of foreign geologists. Trans. geol. soc. London, ser. 2, vol. 5, p. 331-348, 1 text fig., pl. 28.

Nicholson, H. A., & Lydekker, R.

'89. A manual of palaeontology. 3d ed., Edinburgh and London: 2 vols.; illus.

(Vol. 2, p. 1038-1039, fig. 970 *bis*, Chirotherium.)

Oppel, A.

'62. Ueber fährten im lithographischen schiefer. Palaeontologische mittheilungen aus dem museum des königlichen bayerischen staates, pt. 2, 1862, p. 121-125, pl. 39. Stuttgart

(*Ichnites lithographicus* possible track of Archaeopteryx.)

Osborn, H. F.

:00. Reconsideration of the evidence for a common dinosaur-avain stem in the Permian. Amer. nat., vol. 34, p. 777-799, text fig. 1-12.

03a. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. Mem. Amer. mus. nat. hist., vol. 1, pt. 8, p. 451-507, text fig. 1-23.

:03b. *Ornitholestes hermanni*, a new Compsognathoid dinosaur from the upper Jurassic. Bull. Amer. mus. nat. hist., vol. 19, p. 459-464, text fig. 1-3.

Owen, Richard.

'42. [On footprints of upper new red sandstone of Greensell.] Trans. Cambridge philos. soc., vol. 7, p. 355.

Pabst, W.

'96. Die thierfährten in dem oberrothliegenden von Tambach in Thüringen. Zeitschr. d. deutsch. geol. gesellsch. Berlin, vol. 48, p. 808-829, text fig. 1-10, pl. 17-20.

Pictet, F. J.

'53-'57. Traité de paléontologie. 2d ed., Paris: 4 vols., atlas.

(See vol. 1, 1853, p. 406, pl. 20.)

Plieninyer, —.

'38. [On footprints of Stuttgart.] Bericht über der versammlung deutscher naturforscher u. ärzte in Prague, 1837, p. 132-133.

Quenstedt, F. A.

'52. Handbuch der petrefaktenkunde. Tübingen; illus.

(See p. 81.)

'85. Handbuch der petrefaktenkunde. 3d ed., Tübingen. illus.
(See p. 128–133, with figures. A summary.)

Rogers, H. D., *et al.*

'42. Report on the ornithichnites or footmarks of extinct birds in the new red sandstone of Massachusetts and Connecticut, observed and described by Prof. Hitchcock, of Amherst. Ann. and mag. nat. hist., vol. 8, p. 253–258.

Rumpf, —.

'42. [On footprints of Aura on the Saal.] Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1842, p. 450–451.

'43. [On footprints of Aura on the Saal.] Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1843, p. 706–707.

Schwabe, S. H.

'54. [On the footprints of Chirotherium of Altenburg.] Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1854, p. 569–570.

Sickler, F. K. L.

'34. Sendschreiben an J. F. Blumenbach, über die höchst merkwürdigen, vor einigen monaten erst entdeckten reliefs der fährten urweltlicher grosser unbekannter thiere in den Hessberger sandsteinbrüchen, bei der stadt Hildburghausen. Hildburghausen. 4to., 16 pp., illus.

'35. [On the footprints of Hessburg.] Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1835, p. 230–232.

'36. Die vorzüglichsten fährten abdrücke urweltlicher thiere, im buntem sandsteine aus den sandsteinbrüchen der umgegend von Hildburghausen. Hildburghausen.

Smith, G. V.

'84. On further discoveries of the footprints of vertebrate animals in the lower new red sandstone of Penrith. Quart. journ. geol. soc. London, vol. 40, p. 479–481, 1 text fig.

Sollas, W. J.

'79. On some three-toed footprints from the Triassic conglomerate of South Wales. Quart. journ. geol. soc. London, vol. 35, p. 511–516, 1 text fig.
(*Brontozoum thomasi.*)

Struckmann, C.

'80. Vorläufige nachricht über das vorkommen grosser vogelähnlicher thierfährten (Ornithoidichnites) im Hastings-sandsteine von Bad Rehburg bei Hannover. Neues jahrb. f. mineral., geol., u. palaeontol., 1880, vol. 1, p. 124–128, pl. 4.

Tylor, Alfred.

'62. On the footprint of an Iguanodon, lately found at Hastings. Quart. journ. geol. soc. London, vol. 18, p. 247–253, 2 text figs., and diagrams.

Virlet, Th.

'35–'36. Note sur les empreintes de pieds d'animaux dans le grès bigarré des environs de Hildburghausen, en Saxe. Bull. soc. géol. de France, vol. 7, p. 220–224, also note on this paper, p. 260.
(On the Chirotherium tracks of Hessburg.)

Voight, F. S.

'32. [On the footprints of Hessburg.] Almanach der natur, 1832, p. 137.

'35. [On the footprints of Hessburg.] Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1835, p. 322–326.

'36. Weitere nachrichten über die Hessberger thierfährten. Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1836, p. 166–174, pl. 3.

Wagner, —.

'60. [Footprints of *Chirotherium barthi* of Harmerz.] Neues jahrb. f. mineral., geogn., geol., u. petrefaktenkunde, 1860, p. 693.

Wanner, Atreus.

'89. The discovery of fossil tracks, algae, etc., in the Triassic of York county, Pennsylvania. Ann. rept. geol. surv. Pennsylvania, 1887, p. 21–35, pl. 3–13. Abstract in Proc. Amer. assoc. adv. sci., 1888, p. 186.

'92. Fossil tracks in the Trias of York co., Pa. Proc. Amer. assoc. adv. sci., Washington meeting, 1891, p. 286.
(Abstract.)

Ward, Ogier.

'40. [On the footprints of Greensell]. L'Institut, 1840, p. 219.

Warren, J. C.

'54. Remarks on some fossil impressions in the sandstone rocks of Connecticut river. Boston: 54 pp., illus.

'56. [On new remarkable gigantic fossils and footmarks.] Proc. Boston soc. nat. hist., vol. 5, p. 298 306.

Wiegmann, A. F. A.

'35. Thierfährten im bunten sandsteine. Archiv f. naturgesch., 1835, vol. 1, p. 127–131, 395–397.

Williamson, W. C.

'67. On a Cheirotherian footprint from the base of the Keuper sandstone of Daresbury, Cheshire. Quart. journ geol. soc. London, vol. 23, p. 56–57, pl. 3.

Winkler, C.

'86. L'histoire d' ichnologie. Haarlem.

(Historical résumé of the ichnological science, p. 1–187; footprints of Hessburg in the Musée Teyler, p. 188–192, pl. 1–9; impressions in the lithographic limestone of the Musée Teyler, p. 193–200, pl. 11.)

Woodworth, J. B.

'95. Three toed dinosaur tracks in the Newark group at Avondale, N. J. Amer. journ. sci., ser. 3, vol. 50, p. 481–482.

Yates, —.

'38. On the footprints at Liverpool. London and Edinburgh philos. mag., vol. 14, p. 150.

von Zittel, K. A.

'80–'93. Handbuch der palaeontologie. 4 vols. München und Leipzig.

(See vol. 3, 1890, p. 409–411.)

EXPLANATION OF THE PLATE.

PLATE 72.

Figs A and B. *Chirotherium barthi* Kaup. Impressions of the right manus and pes, × $\frac{1}{4}$, with a provisional restoration of the skeleton. Drawn from a photograph of a specimen in the British museum (R. 728).

Figs C and D. *Chirotherium storetonensis.* Impression of the right manus and pes × $\frac{1}{4}$. From specimen no. $\frac{46}{25}$, in the Hitchcock cabinet.

Fig. E. *Otozoum moodii* E. Hitchcock. Imprint of the right manus. × $\frac{1}{4}$. From the type specimen, no. $\frac{5}{14}$, in the Hitchcock cabinet. The bone restoration is highly conjectural.

Fig. F. *Otozoum moodii* E Hitchcock. Impression of the right pes. × $\frac{1}{4}$. Drawn from a specimen preserved in the Geological museum of Amherst college. The specimen has been so trimmed as to destroy most of the web.

Fig. G. *Otozoum moodii* E. Hitchcock. Imprint of the right pes. × $\frac{1}{4}$. From the specimen no. $\frac{4}{4}$, of the Hitchcock cabinet, showing the full development of the web. The broken line (– – – –) indicates the variation between successive tracks of the same foot. The skeleton restoration is somewhat conjectural.

Signs referring to all the figures: ——— pad and web outline; - - - - - - outline of claws; – – – – – outline of variation; – – - – - – restored outline; - - - - - - - - - - broken edge of slab.

INDEX.

Generic and specific names regarded as synonyms are printed in italics. The asterisk (*) indicates the page upon which the species is figured, while that bearing the description of the form is designated by bold faced numerals.

- *Aethyopus*, 501
  - *lyellianus*, 506.
  - *minor*, 501.
- Agriochoerus, 477
- Allosaurus, 471, 492, 493, 543.
- *Amblonyx*, 506.
  - *giganteus*, 512, 513
  - *lyellianus*, 506.
- Amblypus, 481, **530**
  - dextratus, 481, **530**.
- Ammosaurus, 474, 487.
  - major, 489.
- Anchisauripus, 470, 471, 476, 477, 479, **486**, 492, 543, 544, 545.
  - dananus, 470, 479, **487***, 488, 491, 495, 496.
  - exsertus, 479, **489***, 491, 532.
  - hitchcocki, 479, **488***.
  - minusculus, 479, 488, **490***, 522.
  - parallelus, 479, **490**, 491*.
  - tuberatus, 479, **491***, 513, 532.
  - tuberosus, 479, **488***, 522, 532
- Anchisaurus, 471, 474, 477, 487.
  - colurus, 470, 487, 490.
  - polyzelus, 488.
- Ancyropus, 465, 481, **528**.
  - heteroclitus, 481, **529**.
  - *jacksonianus*, 529.
- *Anisichnus*, 482.
  - *gracilior*, 484.
  - *gracilis*, 484.
- *Anisopus*, 482.
  - *deweyanus*, 483.
  - *gracilior*, 484.
  - *gracilis*, 484.
- Anomoepus, 466, 470, 471, 473, 477, 479, 499, **500**, 505, 506, 508, 520, 544, 545.
  - crassus, 479, **503***, 540, 545.
  - cuneatus, 479, **504**.
  - curvatus, 474, 479, **502**, 503*.
  - gracillimus, 479, **504**.
  - intermedius, 470, 477, 479, **501***, 502*, 503, 505, 507, 520.
  - isodactylus, 479, **505***.
  - *major*, 472, 474, 506, 507.
  - minimus, 479, **503**, 504*, 527, 528, 545.
  - *minor*, 500.
  - scambus, 477, 479, **500***, 501, 502, 528
- Anticheiropus, **540**.
  - hamatus, 540, **541**.
  - pilulatus, **540**.
- Antipus, 481, **536**.
  - bifidus, 481, **536**.
  - flexiloquus, 481, **536**.
- Apatichnus, 479, 485, 493, 499, **508**, 509.
  - *bellus*, 485.
  - circumagens, 479, **508***, 509.
  - *holyokensis*, 501, 502
  - minus, 480, **509***.
- Arachnichnus, 481, **538**.
  - dehiscens, 481, **539**.
- Argoides, 465, 480, **518**.
  - isodactyletus, 480, **518**.
  - macrodactylotus, 480, **519**.
  - *minimus*, 518.
  - redfieldianus, 480, 517, **519**.
  - robustus, 480, **519**.
- *Argozoum*, 466, 518.
  - *disparidigitatum*, 519.
  - *paridigitatum*, 518.
  - *redfieldianum*, 519.
- Batrachopus, 464, 465, 473, 479, **482**, 485, 546.
  - bellus, 479, **485**.
  - deweyanus, 479, 482, **483**.
  - dispar, 479, **483***.
  - gracilior, 479, **484**, 485.
  - gracilis, 479, **484***, 485.
- *Brontozoum*, 466, 486, 487, 510, 544.
  - *approximatum*, 511
  - *divaricatum*, 512
  - *exsertum*, 489.
  - *giganteum*, 510.
  - *gracillimum*, 504.
  - *isodactylum*, 501.
  - *loxonyx*, 488.
  - *minusculum*, 490
  - *sillimanium*, 487.
  - *tuberatum*, 491.
  - *validum*, 488.
- *Calopus*, 465
- Cheirotheroides, 479, **485**.
  - pilulatus, 479, **485**.
- Chelonoides, 466, 481, **529**.
  - incedens, 481, **529**.
- Chirotherium, 462, 464, 469, 473, 476, 477, 514, 515.
  - barthi, 462, 471, 473, 514, pl. 72*.
  - storetonensis, 514, pl. 72 *.
- Chlamydosaurus, 473.
- Compsognathus, 471, 497, 544.
- Comptichnus, 481, **538**
  - obesus, 481, **538**.
- Corvipes, 480, 499, **509**.
  - lacertoideus, 480, **510**.
- Cunichnoides, 481, **540**.
  - marsupialoideus, 481, **540**.
- Dimodosaurus, 470*, 471.
- Dryosaurus, 471.
- Eubrontes, 465, 471, 480, 486, 487, 492, 499, 507, **510**, 544.
  - approximatus, 480, **511***, 512, 532.
  - *dananus*, 487.
  - divaricatus, 480, **512***, 517, 519.
  - giganteus, 480, **510**, 511*, 512, 544.
  - *gracillimus*, 504
  - platypus, 480, 507, **512**, 513*.
  - *tuberosus*, 488
- Eupalamopus, 481, **531**, 532.

  dananus, 481, **531**.
Exocampe, 481, **534**.
  arcta, 481, **534**.
  minima, 481, **534**.
  ornata, **534**.
Fulicopus, 465, 472, 479, 499, **505**, 545.
  giganteus, 507.
  lyellianus, 472, 474, 479, **506***, 507*.
Gigadipus, 492.
  caudatus, 492.
Gigandipus, 471, 479, **492**, 493, 543.
  caudatus, 479, **492**, 493*, 509, 511.
  minor, 493.
Gigantitherium, 466, 492.
  caudatum, 492.
  minus, 509.
Grallator, 466, 472, 473, 474, 476, 479, 491, **494**, 496, 521, 544.
  cuneatus, 479, **495**, 496*, 505.
  cursorius, 479, **494***, 495*.
  formosus, 479, **496**, 497*.
  gracilis, 479, 494, **496**, 498, 517, 544.
  gracillimus, 504.
  parallelus, 490.
  tenuis, 479, **495***.
Hallopus, 472.
Harpedactylus, 465, **527**.
  concameratus, 516.
  crassus, 527, **528**.
  gracilior, **528**.
  gracilis, 527.
  rectus, 518.
  tenuissimus, **527**.
Helcura, 481, **530**.
  anguinea, 481, **530**.
  caudata, 531.
  littoralis, 481, **531**.
  surgens, 481, **531**.
Hoplichnus, **541**.
  equus, **541**.
  poledrus, 541.
  quadrupedans, **541**.
Hyphepus, 479, **493**.
  fieldi, 479, **493**.
Hypsilophodon, 471, 499, 507, 545.
Iguanodon, 470.
Isocampe, 481, **537**.
  strata, 481, **537**.
Kadaliosaurus, 546.
Lagunculapes, 480, **525**.
  latus, 480, **525**.
Leptonyx, 498.
  lateralis, 498.
Macropterna, 532.
  divaricans, 532.
  gracilipes, 533.
  recta, 532.
  rhynchosauroidea, 533.
  vulgaris, 533.
Megadactylus, 488.
Mesonyx, 477.
Ornithomimus, 472, 544.
Ornithopus, 466, 522.
  adamsanus, 524.
  gallinaceus, 522.
  gracilior, 523.
  loripes, 525.
Orthodactylus, 481, **535**.
  floriferus, 481, **535**.
  introvergens, 481, **535**.
  linearis, 481, **536**.
Otis, 473.
Otozoum, 466, 468, 472, 473, 475, 480, 499, **513**, 514, 515, 545.
  caudatum, **514**.
  moodii, 472, 480, 495, 511, **513**, 514, pl. 72 *.
  parvum, 480, **515**.
Palamopus, 465, 481, 531, **532**.
  anomalus, 481, **532**.
  clarki, 531.
  dananus, 531.
  divaricans, 481, **532**.
  gracilipes, **533**.
  rogersianus, 481, **533**.
Phalaropus, 470.
  hyperboreus, 470.
Platypterna, 465, 480, **515**.
  concamerata, 480, **516**, 518.
  deaniana, 480, **516**.
  deanianus, 516.
  delicatula, 480, **517**.
  digitigrada, 480, **516**.
  gracillima, 516, 517.
  macrodactylotus, 519.
  recta, 480, **518**.
  tenuis, 480, **517**, 518.
  varica, 516.
Plectropterna, 466, 519, 520.
  angusta, 520.
  elegans, 520.
  gracilis, 528.
  lineans, 528.
  minitans, 501, 520.
Plectropus, 465, 519.
Plesiornis, 466, 476, 480, **521**, 539.
  aequalipes, 518.
  giganteus, 480, **522**.
  mirabilis, 480, **522**.
  pilulatus, 480, **521**.
  quadrupes, 501.
Polemarchus, 465, 480, **520**.
  gigas, 480, **520**.
Ptilichnus, 466.
Rhea, 470.
Sarcorhamphus, 544.
  gryphus, 544.
Sauropus, 465, 501.
  barrattii, 501.
Selenichnus, 476, 479, **498**.
  breviscululus, 479, **499**.
  falcatus, 479, **498**, 499.
Shepardia, 478, 481, **538**.
  palmipes, 481, **538**.
Sillimanius, 465, 480, **522**, 523, 532.
  adamsanus, 524.
  gracilior, 480, **523**.
  rogersianus, 533.
  tetradactylus, 480, 516, **522**, 523.
Stenodactylus, 537.
  curvatus, 537.
Stenonyx, 479, 494, **498**.
  lateralis, 479, **498**.
Steropezoum, 523.
  elegans, 523.
  elegantius, 523.
  ingens, 524.
Steropoides, 465, 480, **523**.
  elegans, 489, **523**.
  elegantior, 523, 524.
  infelix, 480, **524**.
  ingens, 480, **524**.
  loripes, 480, **525**.
  uncus, 480, **525**.
Sustenodactylus, 481, 536, **537**.

curvatus, 481, **537**
Tarsodactylus, 480, **526**.
caudatus, 480, **527**.
expansus, 480, **527**.
Tarsoplectrus, 480, **519**.
angustus, 480, **520**
elegans, 480, **520**.
Toxichnus, **541**
inaequalis, **542**.

Printed April, 1904

Triaenopus, 465, 481, **539**
baileyanus, 481, **539**
emmonsianus, 539
leptodactylus, 539
Tridentipes, 523
elegans, 523
elegantior, 524
ingens, 524
insignis, 525
uncus, 525
Trihamus, **542**.
elegans, **542**
magnus, **542**.
Typopus, **542**.
abnormis, **543**.
gracilis, **543**
Xiphopeza, 480, **526**.
triplex, 480, **526**

INDEX.

Page

- Abies balsamea 448
  - bracteata 447
  - firma 447
  - grandis 448
  - nobilis 447
- Acanthodriles annectens 369
- Acanthophora thierii 56
- Acer carpinifolium 100
  - crataegifolium 100
  - decipiens 101
  - indivisum 101
  - oblongum 100
  - pennsylvanicum 99
  - platanoides 99, 100
  - pseudo platanus 99
  - rubrum 99
  - saccharinum 100
  - saccharum 99
  - spicatum 99
  - tartaricum ginnale 101
  - trilobatum 101
- Aethyopus 501
  - lyellianus 506
  - minor 501
- Agriochoerus 477
- Ailanthus 91
  - glandulosa 96
- Allium cepa 3
  - ursinum 3
- Allosaurus 471
- Amaryllidaceae 2, 3
- Amblonyx 506
  - giganteus 512
  - lyellianus 506
- Amblypus 481
  - dextratus 481
- Ammosaurus 474
  - major 489
- Ampelopsis quinquefolia 97
  - tricuspidata 92, 98
  - veitchii 98
- Amphigenia 341
- Amphiuma 423
- Anagallis 406
- Anatomy of Cassiopea xamachana 191
- Anchisauripus 470
  - dananus 470
- Anchisauripus exsertus 479
  - hitchcocki 479
  - minusculus 479
  - parallelus 479
  - tuberatus 479
  - tuberosus 479
- Anchisaurus 471
  - colurus 470
  - polyzelus 488
- Ancyropus 465
  - heteroclitus 481
  - jacksonianus 529
- Anisichnus 482
  - gracilior 484
  - gracilis 484
- Anisopus 482
  - deweyanus 483
  - gracilior 484
  - gracilis 484
- Anomoepus 466
  - crassus 479
  - cuneatus 479
  - curvatus 474
  - gracillimus 479
  - intermedius 470
  - isodactylus 479
  - major 472
  - minimus 479
  - minor 500
  - scambus 477
- Anthericum liliago 3
- Anticheiropus 540
  - hamatus 540
  - pilulatus 540
- Antipus 481
  - bifidus 481
  - flexiloquus 481
- Apatichnus 479
  - bellus 485
  - circumagens 479
  - holyokensis 501
  - minus 480
- Aquilegia canadensis 93
- Arachnichnus 481
  - dehiscens 481
- Aralia edulis 104
  - sieboldii 104
- Arbacia punctulata 130
- Archaeocalamites 162
- Archirhiza 227
  - [illegible] 227
  - primordialis 227
- Areca 94
  - lutescens 125
- Arenga saccharifera 124
- Argiope 341
- Argoides 465
  - isodactyletus 480
  - macrodactylus 480
  - minimus 518
  - redfieldianus 480
  - robustus 480
- Argozoum 466
  - disparidigitatum 519
  - paridigitatum 518
  - redfieldianum 519
- Asparagus officinalis 3
- Asphodelus luteus 3
- Aspidiophyllum dentatum 110
- Athyris 341
- Atrypa 341
- Aurelia 207, 209
- [illegible] 225
- Batrachopus 464
  - bellus 479
  - deweyanus 479
  - dispar 479
  - gracilior 479
  - gracilis 479
- Batrachoseps 417
- Belamcanda chinensis 3
- Bigelow, R. P. Anatomy of Cassiopea xamachana 191
- Botrychium virginianum 160
- Bowmanites römeri 166
- Brachiopoda, observations on living 313
- Brontozoum 466
  - approximatum 511
  - divaricatum 512
  - exsertum 489
  - giganteum 510
  - gracillimum 504
  - isodactylum 501
  - loxonyx 488
  - [illegible] 490

Page
Brontozoum sillimanium 487
  tuberatum 491
  validum 488
Calamites approximatiformis 183
  cistiformis 183
  ostraviensis 183
  ramifer 183
Calamostachys 166
Calopus 465
Caryota 124, 125
  cumingii 124, 125
  rumphiana 125
  urens 124, 125
Cassiopea andromeda 195
  depressa 195
  frondosa 192
  mertensii 195
  ndrosia 195
  ornata 195
  picta 195
  polypoides 195
Cassiopea xamachana, anatomy and development of 191
Cellulose 1
Chamaerops 127
Cheirostrobus 166
Cheirotheroides 479
  pilulatus 479
Chelonoides 466
  incedens 481
Chimpanzee "Gumbo" 31
Chirodota rotifera 54
Chirotherium 462
  barthi 462
  storetonensis 514
Chlamydosaurus 473
Chrysalidocarpus 124, 125
  lutescens 126
Chrysaora 209
Cingularia 184
Cistella 326
  kowalevskii 335
Cladiscites tornatus 137
Clark, H. L. Synapta vivipara 53
Cleiothyris 341
Cobaea scandens 140
Cocos 124
  weddeliana 125
Colchicum autumnale 3
Comparative anatomy of Coniferales 144
Compsognathus 471
Comptichnus 481
  obesus 481
Convallaria majalis 3
Cooley, G. E. Reserve cellulose of seeds of Liliaceae 1
Corvipes 480
  lacertoideus 480

Page
Corypha 124
Cotylorhiza tuberculata 209, 212
Crania 325
Crocus vernus 3
Cryptobranchus 423
Cucumaria glacialis 59
Cunichnoides 481
  marsupialoideus 481
Cupressus lawsoniana 123
Cyanea 209
Cyclobus oldhami 137
Dactylometra 207
Dahlia variabilis 105
Dallina 329
  floridana 364
  grayii 345
Descriptions of human spines showing numerical variation 237
Desmognathus 417
Development and affinities of Equisetum 155
Dimodosaurus 470
Dionaea 140
Diplothemium maritimum 125
Discinisca lamellosa 322
  stella 323
Dissection and brain of chimpanzee "Gumbo" 31
Dryosaurus 471
Dwight, Thomas. Descriptions of human spines showing numerical variation 237
Dwight, Thomas. Dissection of chimpanzee "Gumbo" 31
Echinoderms, contribution to morphology of 53
Encrinus liliiformis 128
Equisetum, development and affinities of 155
Equisetum arvense 166
  fluviatile 163
  hiemale 166
  limosum 166
  litorale 173
  palustre 168
  silvaticum 173
  telmateia 168
  variegatum 170
Eubrontes 465
  approximatus 480
  dananus 487
  divaricatus 480
  giganteus 480
  gracillimus 504
  platypus 480
  tuberosus 488
Eucharidium grandiflorum 103
Eupalamopus 481
  dananus 481

Page
Exocampe 481
  arcta 481
  minima 481
  ornata 534
Fatsia japonica 104
Foeniculum officinale 6
Footprints, fossil, of Jura-Trias 461
Fossil footprints of Jura-Trias 461
Fraxinus americana 105
  anomala 107
  australis 107
  excessior 107
  oregona 107
  pubescens 107
  sambucifolia 107
Fritillaria imperialis 3
Fulicopus 465
  giganteus 507
  lyellianus 472
Galanthus nivalis 3
Galaxea caespitosa 127
Galtonia candicans 3
Gigadipus 492
  caudatus 492
Gigandipus 471
  caudatus 479
  minor 493
Gigantitherium 466
  caudatum 492
  minus 509
Gladiolus 3
Gleditschia triacanthos 101
Gleichenia 184
Glottidia albida 315
  antillarum 316
  pyramidata 315, 316
Grallator 466
  cuneatus 479
  cursorius 479
  formosus 479
  gracilis 479
  gracillimus 504
  parallelus 490
  tenuis 479
Gymnocladus 91
  disicus 102
Gymnosporangium nidus-avis 118
Hallopus 472
Halonia 161
Harpedactylus 465, 527
  concameratus 516
  crassus 527
  gracilior 528
  gracilis 527
  rectus 518
  tenuissimus 527
Hedera cretacea 105
  helix 104

Page
Helcura 481
anguinea . 481
caudata 531
littoralis . 481
surgens 481
Hemiphlebium . 160
Hemithyris albida . 334
psittacea 331
Hicoria alba . 111
glabra . . 111
ovata . . 110
Holothuria tubulosa 58
Hoplichnus 541
equus . 541
poledrus 541
quadrupedans 541
Hosta caerulea . 3
Human spines showing numerical variation 237
Hydra 127
Hyphepus 479
fieldi 479
Hypsilophodon 471
Iguanodon . . . 470
Iridaceae . . 2, 3
Iris pseudacorus 3
sibirica 3
Isocampe 481
strata 481
Jackson, R. T. Localized stages in development. 89
Jeffrey, E. C. Anatomy and phylogeny of Sequoia . . 441
Jeffrey, E. C. Structure of Equisetum . 155
Juniperus californica 119
communis 119
monospermum 119
virginiana 116
Jura-Trias, fossil footprints of 461
Kadaliosaurus . 546
Kentia 124, 125
balmoreana . 126
Laguncula pes . 480
latus . 480
Laqueus rubellus 331
Larix europaea 116
occidentalis . 116
Latania 124
borbonica . 124
commersonii 124
Lepidechinus rarispinus 132
Lepidodendron harcourtii 161
selaginoides 183
Leptaena rhomboidalis . 341
Leptonyx . . 498
lateralis . 498
Libocedrus decurrens 118, 121
Page
Liliaceae 1, 2, 3
Liliaceae, reserve cellulose in seeds of 1
Lilium martagon [illegible]
Lima 132
Lingula affinis . [illegible]
anatina [illegible]
lepidula . . 315, 318
Liriodendron giganteum . 95
meeki 95
primaevum 95
tulipifera . 93
Living Brachiopoda, observations on 313
Lloydia serotina 3
Localized stages in development 89
Lull, R. S. Fossil footprints of Jura-Trias 461
Lycopodium cernuum 167
clavatum 167
complanatum 169
inundatum . 186
phlegmaria 167
Lytoceras alamaedense 136
Macropterna . 532
divaricans . 532
gracilipes . 533
recta . 532
rhynchosauroidea 533
vulgaris 533
Magellania australis 347
flavescens 360
Megadactylus . . . 488
Melonites multiporus 131
Mesonyx 477
Metacrinus rotundus 127
Morse, E. S. Observations on living Brachiopoda 313
Muscari botryoides . 3
Myrica cerifera 113
Narcissus pseudo-narcissus 3, 4
Necturus, skeletal system of 387
Necturus maculatus 387
punctatus 388
Negundo aceroides . 101
Nelumbium luteum . 169
Numerical variation in human spines 237
Observations on living Brachiopoda 313
Oligoporus missouriensis 131
Onoclea sensibilis . [illegible]
Oreodoxites plicatus 124
Ornithogalum [illegible] 3
Ornithomimus . 472
Ornithopus 406
adamsanus 524
Page
Ornithopus gallinaceus . [illegible]
[illegible] [illegible]
loripes . 525
Orthodactylus . 481
floriferus . 481
introvergens 481
linearis 481
Osmunda . . . . [illegible]
[illegible] . 157
[illegible] [illegible]
Otozoum . [illegible]
caudatum . [illegible]
moodii [illegible]
[illegible] 480
Pachydrilus verrulosus [illegible]
Palaeostachya . [illegible]
[illegible] [illegible]
[illegible] 481
clarki [illegible]
[illegible] [illegible]
[illegible] 481
gracilipes [illegible]
rogersianus 481
Paracalamostachys . 184
[illegible] [illegible]
Pelagia noctiluca 209
[illegible] 128
briareus 128
[illegible] 127
Phalaropus hyperboreus . 470
Phoenicophorum sechellarum 124
Phoenix 96
canariensis 124
dactylifera 5
rupicola . 124
Pholidocidaris meeki 132
Phoronis . . . [illegible]
Phylloceras nilssoni 137
[illegible] [illegible]
[illegible] 161
Phytelephas macrocarpa . 5
Pilema 22
Pinus cembra . 115
densiflora 115
massoniana . 115
monticola 115
[illegible] 115
quadrifolia 115
resinosa . . 11[illegible]
rigida 113
strobus . . 11[illegible]
Placenticeras placenta . 134
Platanus basilobata 110
[illegible] [illegible]
orientalis 109
primaeva . 109
[illegible] 128
Platypterna . . . . [illegible]
concamerata . 480

Page

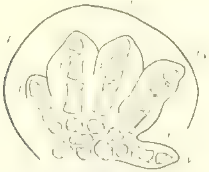
- Platypterna deaniana 480
  - delicatula 480
  - digitigrada 480
  - gracillima 516
  - macrodactylotus 519
  - recta 480
  - tenuis 480
  - varica 516
- Platyzoma 184
- Plectropterna 466
  - angusta 520
  - elegans 520
  - gracilis 528
  - lineans 528
- Plectropus 465
- Plesiornis 466
  - aequalipes 518
  - giganteus 480
  - mirabilis 480
  - pilulatus 480
  - quadrupes 501
- Polemarchus 465
  - gigas 480
- Polyclonia frondosa 192
- Polygonatum multiflorum 3
- Productus 325
- Proteus 388
- Protopterus 423
- Pteris 91
  - aquilina 126, 158
- Ptilichnus 466
- Quercus alba 111
  - chrysolepis 113
  - coccinea 111
  - imbricaria 113
  - minor 111
  - oblongifolia 113
  - tinctoria 111
- Raphis 124
  - flabelliformis 125
  - humilis elegans 125
- Reserve cellulose of seeds of Liliaceae 1
- Rhea 470
- Rhizostoma 225
- Rhus toxicodendron 97
- Rhynchonella 341
- Sabal 124
- Sabelliformis 329
- Salamandra 394
  - maculosa 387
- Sarcorhamphus gryphus 544
- Sassafras sassafras 107
- Sauropus 465
  - barrattii 501
- Sciadopitys 456
- Scilla sibirica 3, 4
- Selaginella laevigata lyallii 160

Page

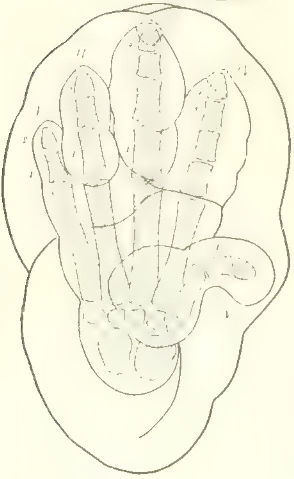
- Selenichnus 476
  - brevisculus 479
  - falcatus 479
- Sequoia, comparative anatomy and phylogeny of 441
- Sequoia gigantea 441
  - langsdorfii 455
  - sempervirens 441
- Sesbania tomentosa 103
- Shepardia 478
  - palmipes 481
- Sigillaria 161
  - diploxylon 184
  - elegans 184
  - pulcherrima 184
  - spinulosa 184
  - vascularis 184
- Sillimanius 465
  - adamsanus 524
  - gracilior 480
  - rogersianus 533
  - tetradactylus 480
- Siredon 411
- Siren 423
- Skeletal system of Necturus 387
- Smilacina racemosa 3
  - trifolia 3
- Smilax auriculata 3
- Sphaerodorum 329
- Sphenophyllum 186
- Spines, human, showing numerical variation 237
- Spondylus 132
- Stenodactylus 537
  - curvatus 537
- Stenonyx 479
  - lateralis 479
- Steropezoum 523
  - elegans 523
  - elegantius 523
  - ingens 524
- Steropoides 465
  - elegans 489
  - elegantior 523
  - infelix 480
  - ingens 480
  - loripes 480
  - uncus 480
- Stevensonia grandifolia 124
- Streptopus amplexifolius 3
- Strongylocentrotus dröbachiensis 129
- Stropheodonta 341
- Strophomena 341
- Sustenodactylus 481
  - curvatus 481
- Synapta digitata 58
  - inhaerens 56
  - lappa 80

Page

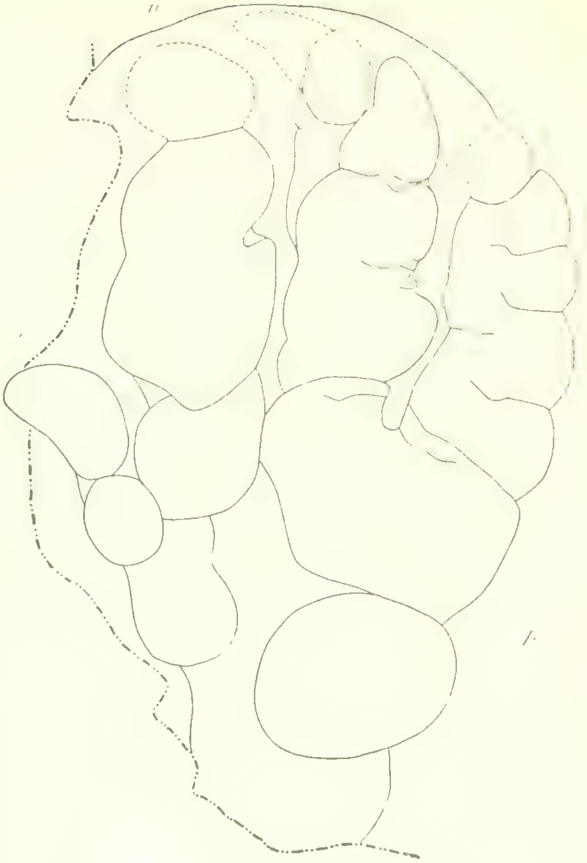
- Synapta picta 55
- Synapta vivipara, morphology of 53
- Synaptula 54
  - vivipara 54
- Tarsodactylus 480
  - caudatus 480
  - expansus 480
- Tarsoplectrus 480
  - angustus 480
  - elegans 480
- Tecoma radicans 105
- Terebratalia coreanica 331
  - minor 331
  - transversa 356
- Terebratula vitrea 358
- Terebratulina caput-serpentis 364
  - septentrionalis 325
- Thecidium 326
- Thuya gigantea 118, 121
  - occidentalis 118, 119
- Todea 156
- Tofieldia calyculata 3
- Toxichnus 541
  - inaequalis 542
- Triaenopus 465
  - baileyanus 481
  - emmonsianus 539
  - leptodactylus 539
- Triarthrus beckii 137
- Tridentipes 523
  - elegans 523
  - elegantior 524
  - ingens 524
  - insignis 525
  - uncus 525
- Trihamus 542
  - elegans 542
  - magnus 542
- Trillium ovatum 3
- Triton 393
- Troglodytes aubryi 31
  - niger 31
- Tulipa gesneriana 3
- Typhlomolge 387
- Typopus 542
  - abnormis 543
  - gracilis 543
- Ulodendron 161
- Variation, numerical, in human spines 237
- Vitis 97
- Waldheimia cranium 325
- Washingtonia 124
- Wilder, H. H. Skeletal system of Necturus 387
- Xiphopeza 480
  - triplex 480



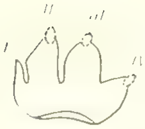
A



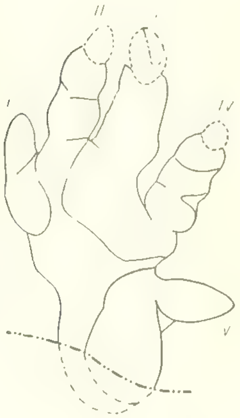
B



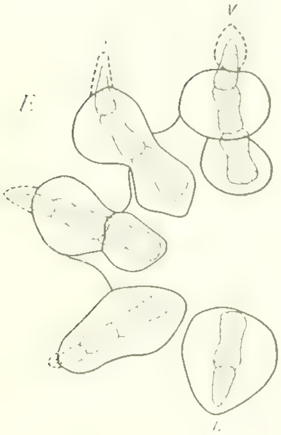
F



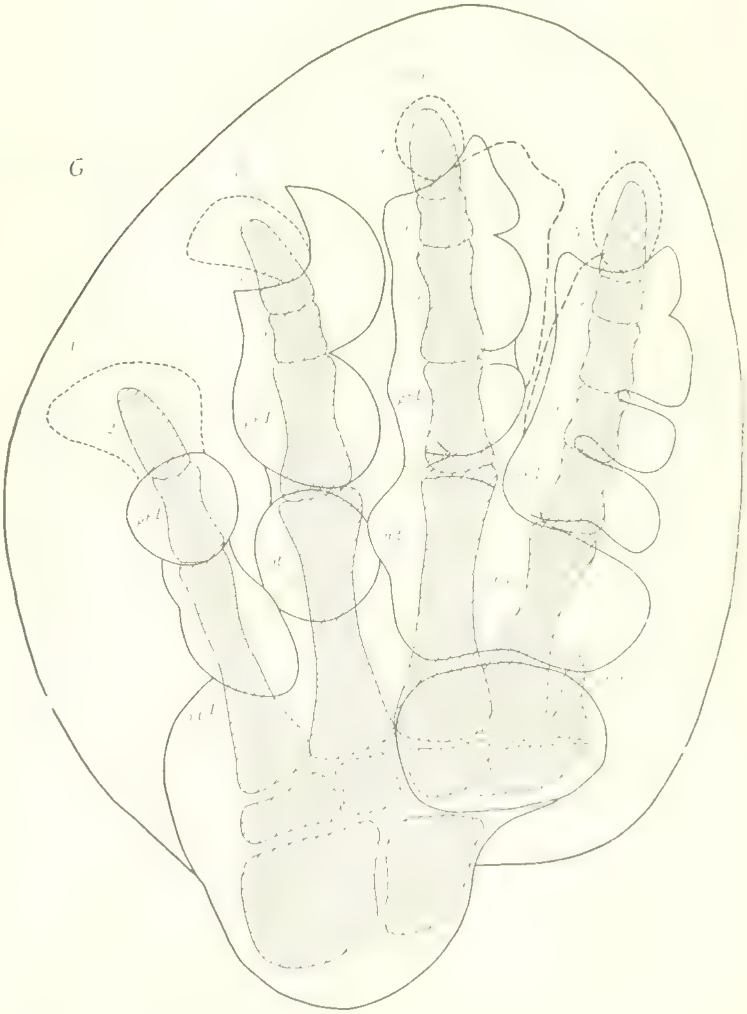
C



D



E



G

LULL ON FOSSIL FOOTPRINTS.

Date D

P Boston Society of Natural History.
Sci Memoirs.
B

v. 5

PLEASE DO NOT REMOVE
CARDS OR SLIPS FROM THIS POCKET

UNIVERSITY OF TORONTO LIBRARY